

A review of the long-term effects of post-harvest silviculture on vertebrate wildlife, and predictive models, with an emphasis on boreal forests in Ontario, Canada

Ian D. Thompson^{a,*}, James A. Baker^b, Michael Ter-Mikaelian^b

^aCanadian Forest Service, 1219 Queen Street East, Sault Ste. Marie, Ont., Canada P6A 2E5

^bOntario Forest Research Institute, Ontario Ministry of Natural Resources, 1235 Queen Street East, Sault Ste. Marie, Ont., Canada P6A 5N5

Received 19 December 2001; accepted 6 August 2002

Abstract

Greater fibre yields may be possible in commercial forests through an increased application of post-harvest silvicultural techniques. In Canadian boreal forests, while basic silvicultural regeneration techniques such as planting, seeding, scarifying, and tending, have been employed since the 1940's, more intensive techniques (intensive forest management (IFM)) such as increased area planted, pre-commercial and commercial thinning, extra tending events, fertilizing, and short rotations may soon be used. There may be effects of basic and more intensive silviculture on biodiversity in the long-term, compared to natural regeneration following logging or especially stand development following natural disturbances. We reviewed approximately 50 papers that reported studies of the long-term effects of post-harvest silviculture on vertebrate wildlife. In particular, large impacts to biodiversity universally occur when native forest types are replaced by rapidly-growing exotic tree species. However, in boreal forests, native tree species are usually planted, and so any effects on associated wildlife communities may be considerably less than in non-native species plantations. Limited long-term information is available, but published studies of effects of basic silviculture and IFM suggested that loss of structures in forest stands was an important common impact that resulted in vertebrate species responses. Fewer structural features in managed forests compared to in natural forests likely results in reduced numbers of animal species dependent on those structures, such as cavity-using species and species for which large decaying woody debris is important. Simplifying stand structures and species composition may result in systems with low connectivity, making them vulnerable to insect and mammalian herbivory. Concentration of IFM in stands on highly productive sites could exacerbate effects (positive or negative), owing to the positive relationship between forest productivity and animal and plant diversity. Species such as black-backed woodpeckers (*Picoides arcticus*) may be reduced over large areas by stand conversion to mixedwoods, stand structural changes and especially age-class truncation. On the other hand, IFM may contribute increased habitats to species favoring young to mature coniferous-dominated forests, that normally decline across a landscape following clearcutting in boreal mixed and upland conifer stands. An aspatial model, based on published and local information and expert opinion, suggested that IFM and post-harvest silviculture in Ontario's boreal forests would produce positive and negative species-specific effects on the vertebrates that we modeled. However, IFM appeared to result in little increased effect over basic post-harvest silviculture. We also expect that stand-level effects of IFM on species would accumulate through time over landscapes, as more stands come under intensive management and the level of effects will be cumulative.

Crown Copyright © 2002 Published by Elsevier Science B.V. All rights reserved.

Keywords: Intensive forest management; Biodiversity; Birds; Mammals; Amphibians; Boreal forest; Ontario

*Corresponding author. Tel.: +1-705-541-5644; fax: +1-705-541-5700.
E-mail address: ithompso@nrcan.gc.ca (I.D. Thompson).

1. Introduction

There are explicit expectations in long-term forest management planning that the use of post-harvest silviculture will enable increased production of wood on intensively managed forest lands. Intensively managed forest lands might be used to offset areas removed from production under various forms of protection, such as parks. In the province of Ontario, Canada, for example, the Ontario Forest Accord (an industry-government forest land management agreement) suggests that increased yields from crown forests can be achieved by using intensive forest management (IFM) to compensate for lands that were newly designated as protected under the Accord.

This review paper is intended to provide a background to understanding the possible effects at the forest stand and landscape scales of the cumulative impacts of applying basic silviculture and IFM over time, on vertebrate animal diversity in boreal forests in Ontario. Our second objective is to model the possible long-term effects of IFM for selected vertebrates. We have adopted the definition of IFM from Bell et al. (2000) that IFM is “aimed primarily at increasing the value and/or volume of desired [fiber] forest components”. In this review, we refer to basic silviculture as normal post-harvest silvicultural practices including tending once (chemical or mechanical), planting, seeding, and site preparation including by herbicide application, prescribed burning, or scarification. Intensive silviculture includes any treatment, following a

harvesting operation and additional to basic post-harvest silviculture, that is intended to further direct forest succession, spacing, growth rate, and/or species composition, including age-class truncation, and falls into two main types: intensive and elite. Intensive refers to improved basic post-harvest silviculture including possible multiple applications of herbicides, thinning, and more careful matching of planting stock and seed to site. Elite silviculture refers to site and tree improvement, as well as intensive management, and includes techniques such as fertilization, drainage, and planting genetically altered stock. These latter techniques may become more frequent in the future in Ontario, in an attempt to increase production to compensate for productive forest assigned to protected areas. In our estimation of effects, we have not distinguished between intensive and elite post-harvest silviculture, and refer to them together as IFM.

The managed boreal forest and the Great Lakes, St. Lawrence forest regions together cover more than 64 million ha of Ontario. Prior to 1970, very little of the area harvested in the province was treated but the proportion has increased since then, and appears to have stabilized at between 30 and 40% of the area harvested by 1990 (Fig. 1) (Carleton, 2000, and Ontario Ministry of Natural Resources, unpublished data). The actual area treated is slightly higher because areas treated following selection or shelterwood harvesting, typical logging practices in many Great Lakes, St. Lawrence types, are not included in these figures. Carleton (2000) summarized information pertaining

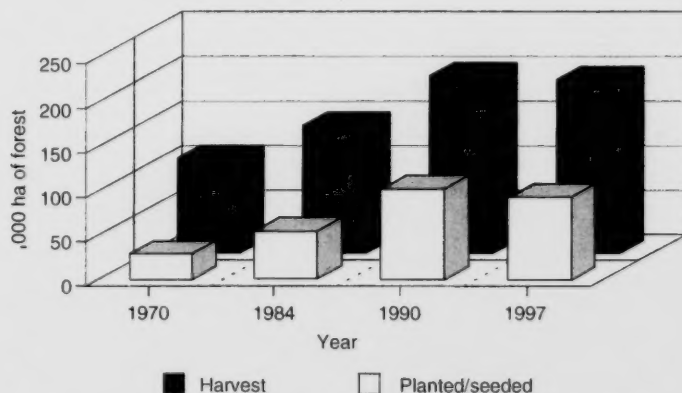


Fig. 1. Area of boreal forest harvested and planted and/or seeded in Ontario, during selected years from 1970 to 1997 (data from Ontario Ministry Natural Resources).

Table 1

Generalized regeneration trajectories following clearcut harvesting with and without basic silviculture (treated), and natural wildfire in boreal forests, based on Hearnden et al. (1992), Carleton (2000), and Thompson (2000)

Original stand	Most common resulting stand types following		
	Logging	Logging + treated	Natural disturbance
Upland black spruce ^a	Hardwood, mixedwood	Mixedwood	Black spruce, mixedwood
Lowland black spruce	Alder	Alder/black spruce/balsam fir	Black spruce
Jack pine	Mixedwood, jack pine	Jack pine, mixedwood	Jack pine
Mixedwood	Hardwood	Mixedwood, mixed conifer	Mixedwood
Mixed conifers	Mixedwood, mixed conifer	Mixedwood, jack pine	Jack pine, mixed softwood

^a Black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), Alders (*Alnus* spp.), balsam fir (*Abies balsamea*).

to regeneration patterns with and without treatments in boreal forests. He noted that regardless of whether areas are planted or not, a high proportion of logged upland spruce (*Picea* spp.) and jack pine (*Pinus banksiana*) has been converted to hardwood or mixedwood stands (Table 1). In the case of jack pine, basic silviculture has resulted in a greater proportion of stands returning as jack pine, than under natural regeneration following logging, but less than if the stands had burned. Another change in stand type following logging has been a decline in the area of mixed conifers (usually black spruce [*Picea mariana*] and jack pine) on uplands. While the result of natural regeneration and basic silviculture on those sites is most often mixedwoods, a much greater proportion are returned as only or predominantly jack pine under basic silviculture than on untreated sites. Natural types following fire on upland mixed-conifer sites are predominantly mixed softwoods, black spruce, or jack pine (Thompson, 2000). In general, Carleton (2000) noted that there are substantial differences among possible outcomes after logging in boreal forests, with a general trend away from original conifer forest to mixedwoods and hardwoods, with a notable decline in white spruce (*Picea glauca*).

Tree species that have increased in abundance as a result of forest management in Ontario forests (whether basic silviculture has been applied or not) are balsam fir (*Abies balsamea*), red maple (*Acer rubrum*), and aspens (trembling aspen [*Populus tremuloides*], large-toothed aspen [*P. grandidentata*], and balsam poplar [*P. balsamifera*]) (Carleton, 2000). As a general statement, basic silviculture increases the density of conifers in a stand as compared to natural regeneration following logging for most stand types.

For example, in Maine, areas treated with glyphosate had double the number of regenerating conifers 11 years following treatment (regardless of height), than was recorded on untreated control plots (Eschholz et al., 1996). Species whose abundance is increased by basic post-harvest silviculture, compared to natural regeneration following logging, include: red pine (*Pinus resinosa*), white pine (*P. strobus*), black spruce, white spruce, and jack pine (Carleton, 2000; Thompson, 2000; Hearnden et al., 1992). At broad scales and over time, an important effect of post-harvest silviculture will be the amount of forest converted from one forest type to another. Effects on biodiversity would be expected especially if certain ecosystem types are generally changed, if there are differences in landscape structure vs. a natural post-disturbance system, and/or if considerable truncation of age-classes occurs in intensively managed forests.

We were interested in the longer-term effects of forest change as a result of IFM and so this review excluded studies that examined only the early post-treatment effects (defined here as the shrub stage), and studies that provided information on small-scale impacts such as one stand or on small experimental plots. Short-term effects of IFM or basic post-harvest silviculture occur on small portions of the landscape (individual stands), affect small numbers of animals and plants for a short time period, and hence are likely transitory (for example, see Sullivan and Sullivan, 1982; Lautenschlager, 1993; De Bellefeuille et al., 2001). We have not included studies that discussed the trivial comparison between young stands regenerating following basic silviculture or IFM, and nearby old primary forest. We also did not consider the many reported studies of small plantation forests

in agroforest landscapes, because of fragmentation effects in discontinuous forest patches, and long-term multiple disturbances on such landscapes. Finally, we did not include studies for which forest stand variables were not reported, because we could not determine adequacy of the control stands. Under our criteria, about 50 papers that specifically reported testing the effects of basic silviculture or IFM were used for this review, while about 80 articles were excluded.

The literature is replete with studies reporting negative impacts on local fauna resulting from the replacement of native forests with plantations of exotic tree species (e.g. Lamothe, 1980; Clout and Gaze, 1984; Norton, 1998; Estades and Temple, 1999; Lindenmayer et al., 1999; Magura et al., 2000). These studies have universally shown reductions in most vertebrates (and invertebrates) compared to their populations in natural primary forests. In some cases natural deciduous forests are replaced with exotic conifers (e.g. Estades and Temple, 1999), while in others effects are associated with replacement of local conifer species with non-local or exotic conifers (e.g. Peterken et al., 1992; Gjerde and Saetersdal, 1997). However, an important difference in boreal forests is the almost exclusive use of native species in intensively managed forests, compared to the more common use of exotic species in many temperate and tropical regions. Hence in intensively managed northern areas, any effects on animals are not related to responses to novel tree species. We have primarily limited our review to studies where intensive management involved native species and the conclusions appeared to be applicable in a general sense, although we have included some studies in exotic plantations to illustrate common animal responses to change. Our review is organized by the vertebrate species groups for which effects were tested.

2. Effects of post-harvest silviculture on vertebrates

2.1. Birds

We expect basic silviculture and IFM to affect bird communities as a result of changes in habitat structure (vertical and horizontal diversity, individual structures, patchiness of habitats, edge creation, and

individual patch sizes), and plant successional changes, compared to natural regeneration. A review by Wedeles and Van Damme (1995) reported no information on the long-term effects of basic silviculture on birds, especially for boreal forests. They discussed the short-term effects on birds of deciduous shrub removal by herbicides and the consequential changes in habitat structures. In the longer-term, they suggested (but left unspecified) negative impacts from treatments that simplified forest structure, including plantation forests on sites that had been mixedwoods prior to logging, reduction of hardwoods by herbicides in favor of conifer-dominated forests, and the loss of snags during scarification operations. Lautenschlager (1993), reviewed the impacts of herbicides on wildlife, but found no studies that considered long-term effects on songbird habitats.

Under IFM, a stand is usually harvested when it is mature, before enters a gap-dynamics phase common in old-growth forests. The cumulative effect, across a landscape, of the truncation of age in forest stands under basic silviculture or IFM may have important impacts in the long-term on species that breed optimally in older stands. Concerns for impacts on avian diversity from truncation of forest age were discussed for plantation forests in Britain by Peterken et al. (1992), and in Belgium by Baguette et al. (1994). They suggested that a suite of species including red crossbills (*Loxia curvirostra*), blue tit (*Parus caeruleus*), pied flycatcher (*Ficedula hypoleuca*), goshawk (*Accipiter gentilis*), siskins (*Carduelis carduelis*), and redpolls (*Carduelis flammea*), among others, only become established in stands at about the time the forest is liquidated, in early maturity. National-level populations of these species were low owing to limited habitat availability, and the lack of older forests precluded existence of some additional species that were once present in Britain but were extirpated. Truncation of forest age, prior the old growth stage, has also been noted as potentially limiting to some avian species in boreal forests in Canada by Setterington et al. (2000) and Thompson et al. (1999) in Newfoundland, by Imbeau et al. (1999) and Drapeau et al. (2000) in Quebec, and by Kirk and Hobson (2001) in jack pine stands of northern Saskatchewan. These five studies noted in common that black-backed woodpeckers (*Picoides arcticus*), three-toed woodpeckers (*P. tridactylus*), and brown creepers (*Certhia americana*)

might be most affected by a reduction in old coniferous boreal forests. The importance of maintaining old forests for certain bird species has also been well documented in many other North American studies (e.g. Ruggiero et al., 1991; Brawn et al., 2001). Monkkonen and Welsh (1994) suggested that loss of large expanses of mature coniferous forest would have an impact on boreal chickadee (*Parus borealis*) and perhaps pine siskin (*Carduelis pinus*) populations, as these species may select habitats at a forest landscape scale. In Great Lakes forests in Ontario, work by Simard (2001) indicated that red crossbills (*Loxia curvirostra*) require high density (>40% white pine [*Pinus strobus*], ca. 100 stems/ha) old pine forests to breed successfully, and that age truncation and commercial thinning would have an effect at the population level as a result of reduced seed (food) availability.

An important impact of site preparation is snag removal during either scarification or prescribed burning. A lack of snags in older planted forests may limit species that require cavities to nest (Wedeles and Van Damme, 1995). Enns (1994) reviewed the limited information that exists on effects of mechanical site preparation, including a number of immediate post-treatment studies in British Columbia, Canada. She suggested that a reduction in shrubs would affect food for wildlife species such as moose (*Alces alces*), deer, and fruit-eaters such as American robins (*Turdus migratorius*), sparrows, ruffed grouse (*Bonasa umbellus*), and waxwings.

Sullivan (1985) reported only short-term effects of herbicide use on breeding birds in west coast plantation forests. In Norway, Eggstad et al. (1988) found that male black grouse (*Tetrao tetrix*) avoided conifer plantations that had been sprayed with glyphosate, 6 years following the spraying, probably because of reduced vertical cover density. However, these authors also found that the hens used the sprayed blocks equally with the unsprayed controls. No clear results have been achieved from the few retrospective studies of the longer-term effects of herbicides on vertebrate wildlife that have been conducted partly as a result of inappropriate experimental design that did not include pre-spray conditions (Lautenschlager, 1993).

Moore and Allen (1999) stated that early crown closure reduced avian species richness in plantation forests, but that later thinning of the trees could offset

the effect (Chritton, 1988). Vertical diversity resulting from a deciduous sub-canopy layer strongly influenced bird richness and abundance in plantation forests in Scotland (Moss, 1978). In Arkansas, USA, Barber et al. (2001) reported significantly greater loss of songbird nests to predators in planted vs. natural forests. However, Bunnell et al. (1999), in their general review of forest management in British Columbia, stated that thinning in western pine or fir forests seemed to produce little effect on use by bird species, but that this was likely related to the lack of deciduous trees invading those thinned stands.

In aspen plantations in the Great Lakes States and Ontario, those stands embedded in natural forests supported fewer generalists and maintained bird communities that were more like those in the natural forest, than stands that were isolated in mostly agricultural landscapes (Christian et al., 1998). In Wisconsin, Cooper's hawks (*Accipiter cooperii*) were as productive in red pine and white pine plantations as they were in natural forests (Rosenfield et al., 2000). A survey in closed red pine plantations compared to a nearby mature mixedwood in central Ontario, indicated only one breeding pair of birds in the red pine, compared to 18 species in the natural stand (MacDonald, 1965). Work in eastern Ontario red pine plantations reported that there was a positive relationship between bird species richness and the number of deciduous trees in the stand (Plosz, 1994; Robertson and Kristensen, Queen's University, personal communication).

The longest history of planted forests is from Europe. An early study from southern Sweden by Nilsson (1979) compared old plantation forests of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) to the natural mixedwood forests of oak and Norway spruce. He found that the natural forest maintained about three times more birds, and that especially the cavity-nesters (≤ 6 times more) and warblers (≥ 6 times more) were most abundant in the natural stands. Six species, including two cavity-nesters, were only found in the natural forest, while two species, one of which was the panboreal red crossbill, were only found in the plantation stands. No suggestion was provided as to why the differences occurred. In northern Finland, differences between natural forests and old plantation stands, which both conifer-dominated, were much less marked, although cavity nesters were

also reported in lower numbers in plantations (Haa-penen, 1965). However, 25 years later, declines in other species (such as tits and jays) were found by Virkkala (1991) for the same forests, as a result of reduced forest age in general and decreased area of primary forest which had probably provided source populations of some bird species for surrounding areas. In Norway, where about 13% of the native Scots pine forest had been replaced by Norway spruce plantations, Gjerde and Saetersdal (1997) reported fewer species in spruce forests, but that avian diversity increased in landscapes with mixtures of the two trees. Hole-nesters generally declined in all of the plantation forests. Another cavity-nester, the boreal owl (*Aegolius funereus*), is significantly affected by the availability of natural cavities, but appears to respond well to supplementary nest boxes in Finland (Hakkarainen et al., 1997). Current concerns in Scandinavia pertain to species such as capercaillie (*Tetrao urogallus*), hazel grouse (*Bonasa bonasia*), Siberian tit (*Parus cinctus*), pine grosbeak (*Pinicola enucleator*), Siberian jay (*Perisoreus infaustus*), great spotted woodpecker (*Dendrocopos major*), and three-toed woodpecker. These species require large areas of older forests that are beyond rotation age, but have been substantially reduced under the forest management regime of wide-spread short-rotation plantation forestry (Virkkala, 1991; Angelstam, 1990, 1992; Edenius and Elmberg, 1996; Mikusinski and Angelstam, 1997; Gjerde and Saetersdal, 1997).

Temple et al. (1979) suggested that the occurrence of certain bird species could be predicted in the central North American Great Lakes—St. Lawrence forest biome, based on effects of basic silviculture on tree species composition and size. For example, they predicted that increased pine would result in increased abundance of pine warbler (*Dendroica pinus*), red-breasted nuthatch (*Sitta canadensis*), hermit thrush (*Catharus guttatus*), blackburnian warbler (*D. fusca*), and Nashville warbler (*Vermivora ruficapilla*), and that increased spruce would lead to more Swainson's thrushes (*Catharus ustulatus*), yellow-bellied flycatchers (*Empidonax flaviventris*), American redstarts (*Setophaga ruticilla*), and blackburnian warblers. They also suggested that a higher density of trees per unit area would lead to more scarlet tanagers (*Piranga olivacea*) and ovenbirds (*Seiurus aurocapillus*), while larger trees should increase the number of

pileated woodpeckers (*Dryocopus pileatus*) and solitary vireos (*Vireo solitarius*).

At the stand level, several authors have suggested that, while differences between avian communities in early successional and plantation forests occur, such differences disappear by the time the stands attain maturity (Dickson et al., 1993; Hansen et al., 1995; Barber et al., 2001). Other research indicated differences in densities of cavity-nesting species in mature planted and natural forests because of reduced structure in the former (e.g. Repenning and Labinsky, 1985; Land et al., 1989). Although stand-level differences may be observed, several studies have indicated that populations of most songbird species appeared sustainable, across a large landscape despite a long history of management (e.g. Morrison, 1992; Welsh and Healy, 1993; Yahner, 2000; Wigley et al., 2000). On the other hand, Pimm et al. (1995) discussed recent past eastern North American avian extinctions, present numbers of vulnerable species, and warned of an impending 'extinction debt' that likely exists owing to ongoing large-scale habitat changes. Similarly, in Europe, Edenius and Elmberg (1996) reported that increased pine (and decreased mixedwoods forests) in Swedish forests as a result of intensive management, has led to a decreased abundance and richness of forest birds (especially Siberian species and tree pipits [*Anthus trivialis*]) at a landscape scale, as a direct consequence of the reduction in available habitat. The possible effects of IFM on birds may be dependent on extent of the area managed at a forest landscape scale, the ability to maintain structures at the stand scale, and management objectives that dictate the forest rotation age and amount of old forest of various types within the landscape.

2.2. Mammals

There is considerably less information about the effects of post-harvest silviculture for mammals than is available for birds. Wedeles and Van Damme (1995) reported no long-term studies of the effects of any post-harvest silviculture on mammals, and speculated that most changes would be short-term, affecting mammals only during early phases of forest development.

No information exists on the long-term effects on mammals of mechanical site preparation in boreal forests. Two studies from Alberta, Canada, showed that browse production is reduced following scarification,

resulting in lower use of treated sites than untreated sites by moose, white-tailed deer (*Odocoileus virginianus*), and elk (*Cervus elaphus*) (Stelfox and Cormack, 1962; Stelfox et al., 1976). Enns (1994) suggested that the lack of fruit production in early successional stages as a result of scarification would reduce use by species that feed on berries, such as black bears (*Ursus americanus*) and chipmunks (*Eutamias* spp.). Scarification reduces the amount of woody debris, which is an important habitat component for many small mammals (Carey and Johnson, 1995). In particular, red-backed voles (*Clethrionomys gapperi*) are related to the amount and quality of decaying coarse woody debris (Nurdyke and Buskirk, 1991; Bowman et al., 2000; Moses and Boutin, 2001).

Conifer release was studied by Sullivan (1985) in British Columbia, where he found minor transitory effects of glyphosate application on feeding by black-tailed deer (*Odocoileus hemionus*) and small mammals in 10–20-year-old plantations. In Maine, moose browse declined following spraying but later recovered, so that by 7–11 years later, the amount of browse exceeded that on untreated areas (Newton et al., 1989; Raymond et al., 1996). In another long-term assessment of the effects of glyphosate, Sullivan et al. (1997) reported no effects on small mammal populations or species composition, 9 and 11 years following application for conifer release in Douglas fir (*Pseudotsuga menziesii*) plantations in British Columbia. However, in Norway, the use of plantations by hares (*Lepus timidus*) was reduced up to 10 years after spraying with glyphosate (Hjeljord et al., 1988). Effects of herbicide spraying appear to be species specific, reflecting individual life histories, habitat preferences, and food requirements.

A comparison of Englemann spruce (*Picea engelmannii*)–subalpine fir (*Abies lasiocarpa*) sites in western Canada, that had been clearcut and regenerated naturally, to similar sites that had been cut and prescriptively-burned, showed minimal effects of the burning on small mammal communities 12 years following the treatment (Sullivan et al., 1999). A significant response was only seen in one species, long-tailed vole (*Microtus longicaudus*), which was significantly less abundant on the burned sites than on unburned sites. Thinning in 20-year-old lodgepole pine (*Pinus contorta*) plantations resulted in no change in use or production in red squirrels (*Tamiasciurus*

hudsonicus) in Alberta, Canada (Sullivan and Moses, 1986).

Truncation of forest age by short rotations could affect certain mammals species favouring older forests, such as marten (*Martes americana*) and woodland caribou (*Rangifer tarandus*) for which old forests may provide optimal habitats (Thompson, 1994; Schaefer and Pruitt, 1991). Negative effects of forest age reduction have been reported for sciurids in the US Pacific northwest, primarily as a result of limited structural or ground cover development within the younger stands (Carey, 2000). The significance of any age truncation effect from IFM requires a landscape perspective, and would be dependent on the amount of old forest available within the broader forest landscape.

2.3. Amphibians

Among the vertebrates, least information is available for impacts of forest management on amphibians (or reptiles). In fire-driven ecosystems, Russell et al. (1999) suggested that in the long-term, prescribed burning could help maintain amphibians in managed forests by sustaining some of the natural processes of ground cover development. DeMaynadier and Hunter (1995) expected that basic silviculture, especially the conversion from mixedwoods or deciduous forests to coniferous forest plantations, would reduce richness and density of amphibians as a result of decreased pH, reduced litter depth, and loss of coarse woody debris. Two studies of salamanders in plantation forests supported those predictions, although the plantation forests studied were young (25 years) and were compared to much older natural-origin forest (Bennett et al., 1980; Pough et al., 1987). On the other hand, correlations of amphibian numbers with amounts of coarse woody debris were equivocal in regenerating and primary western coastal forests (Bunnell et al., 1999; Aubry, 2000), suggesting that in those forests at least, there always is sufficient wood on the ground to not limit persistence of populations.

3. Summary of inferred stand and landscape changes in important variables

At the stand level, the most intrusive effects of basic silviculture on biodiversity would occur cumulatively

as a result of the full suite of post-harvest activities including scarification, planting, followed later by herbicide application(s). The various studies that we reviewed suggested some key variables to which the various vertebrate species respond may be altered by basic silviculture or IFM. IFM would likely produce additive effects to those from basic silviculture, although the magnitude may not necessarily be large.

Large snags and cavity trees (living or dead) are used for perching by avian predators while hunting, as nesting sites for primary and secondary cavity nesters, and as dens by many mammals including bats, squirrels, and mustelids. Often, many small snags remain following harvesting, and the total snag density can be higher in a young stand, than in a mature stand following original logging (e.g. Hansen et al., 1991). However, it is generally large sturdy snags that are important to vertebrate wildlife as denning and nesting sites (e.g. Thomas et al., 1979; Kirk and Naylor, 1996; Jung et al., 1999). Many snags left following logging may be removed during scarification, prescribed burning, or may blow over before surrounding trees grow, and these trees usually occur at low densities in second-growth stands until the stands have aged well into the mature stage. Hansen et al. (1991) found significantly fewer large trees and large snags in 80–100-year-old managed versus natural forests in the Pacific Northwest, and suggested that snags, and woody debris, would decline considerably with each subsequent rotation.

The amount of woody debris in a forest stand varies with age, origin, disturbances, and forest type. In managed stands in boreal and Great Lakes—St. Lawrence forest, woody debris can be abundant immediately following logging and for the subsequent 15–20 years, as a result of felled unmerchantable stems, rotted lower boles, and tops left on site (e.g. Duvall and Grigal, 1999; Potvin et al., 2000). In boreal forests, much of this material is aspen and white birch that rapidly rots. Further, early rotation of stands will continually reduce woody debris in each subsequent stand (e.g. Hansen et al., 1991), as woody debris is most abundant in older forests (Thompson, 1994; Thompson and Curran, 1995; Sippola et al., 1998; Siitonen et al., 2000). Duvall and Grigal (1999) found that managed red pine forests always had less coarse woody debris than did unmanaged stands. This does not mean that intensively managed stands could

not eventually accumulate significant amounts of coarse woody debris, but they would only be likely to do so if they were permitted to grow into a gap-phase state.

The quality of the woody debris in terms of size and state of decay is important for wildlife habitats for cover, feeding areas, and den sites (e.g. Pough et al., 1987; Buskirk et al., 1989; Sippola et al., 1998; Aubry, 2000; Bowman et al., 2000), possibly more so than is quantity of woody debris (Aubry, 2000). A range of woody debris from solid to almost completely decomposed and moss-covered is normally found in natural mature forests, although most large decaying wood occurs in old-growth forests (Thomas et al., 1979). Salamanders, shrews, and some vole species require large and/or moist and decaying woody debris as denning, hunting, resting, or breeding habitat (Clough, 1987; Pough et al., 1987; Nordyke and Buskirk, 1991; Wilkins and Peterson, 2000; Bowman et al., 2000). Some boreal carnivores such as, marten and fisher (*M. pennanti*), use large diameter woody debris as dens (Banfield, 1974; Buskirk et al., 1989). These dens may be natal sites, and hence important at the population level (Henry and Ruggiero, 1993). A common practice during scarification is to push woody debris into windrows. As a result, although the volume of debris may not change on a per hectare basis, its value to many wildlife species may be greatly diminished because it is concentrated in small areas rather than spread across the forest floor much is located away from the ground, and the material has reduced moisture content. Nevertheless, Pough et al. (1987) noted that these piles made excellent habitat for efts of the red-backed salamander (*Plethodon cinereus*). Woody debris is also eliminated during prescribed burning following logging, while wildfires in older forests create an abundant source of new debris, as fire-killed trees continually fall through time. Forest management can reduce the quality and quantity of woody debris compared to in natural-origin forests from pole stage to older stands, and this can be further affected by some post-harvest silviculture practices, with consequent effects for certain vertebrates (e.g. Hansen et al., 1991; Bowman et al., 2000).

A multi-story canopy and a deciduous shrub understory (complex vertical diversity or foliage height diversity) are important variables affecting songbird

populations, suggested in many studies (e.g. MacArthur and MacArthur, 1961; Welsh and Lough-
heed, 1996; Willson and Comet, 1996). A high value for
this variable can be produced by a mixture of con-
iferous and deciduous species within a stand, resulting
from different growth rates and forms, with light
penetration to the forest floor at all stand ages. Boreal
and temperate mixedwoods stands support some of the
conifer specialist and deciduous specialist species, as
well as many generalist avian species (e.g. De Graaf
et al., 1998). However, intensively managed plantation
forests can be highly uniform in species and tree age,
with a reduced vertical and horizontal structure, and
generally maintain uniform closed canopies compared
to natural forests. A reduced heterogeneity of tree
species results in lower niche space and reduced
richness of associated plant and animal species
(Moore and Allen, 1999; Repenning and Labinsky,
1985). Conifer release by mechanical or chemical
methods accelerates succession toward conifer-domi-
nated stands, and pre-commercial thinning removes
many of the deciduous trees resulting in long-lasting
effects on stand structure by reducing existing and
potential cavity trees, eliminating fruit-bearing spe-
cies, and altering successional canopy structure in the
stand. Some authors have suggested that commercial
thinning in conifer plantations could improve vertical
structure if the stands are subsequently invaded by
deciduous trees and shrubs following the partial har-
vesting (e.g. Plosz, 1994). In such cases, a curve
depicting forest bird richness over time would
decrease from early crown closure, and increase again
later into maturity once the thinning was done. Multi-
story canopies occur least in even-aged conifer and
mixed conifer forests that form following logging and
basic silviculture, or following burning of black spruce
and jack pine forests. Clearcutting in boreal mixed-
woods is likely to result in natural regeneration to
deciduous-dominated stands (Carleton and MacLel-
lan, 1994; Carleton, 2000), and planting conifers
followed by tending with herbicides can be employed
to maintain mixed stands, and multi-storied canopies,
on such sites. Further, the few studies that have been
done suggested that the effects of herbicides used for
conifer release in natural or artificially-regenerated
stands cannot be detected once the stands mature (i.e.
after 40–60 years) (e.g. Moore and Allen, 1999). Fire
is the major natural disturbance in Ontario forest

ecosystems (Baker et al., 1996; Carleton, 2000),
and so the use of prescribed burning at 'normal' fire
intervals may be beneficial in maintaining a diverse
understory and contributing to plant and vertebrate
species diversity in managed stands, as has been
reported for several other forest systems (Russell
et al., 1999).

Reviews by Rochelle and Bunnell (1979), Kimball
and Hunter (1990), Moore and Allen (1999), and
Hartley (2002) suggested that mechanical site pre-
paration fosters increased plant richness compared to
following a herbicide application, but a lower diversity
than in naturally regenerating forests. Types of ground
covers can influence the use of stands by vertebrates.
For many small vertebrates, ground covers affect the
abundance of their principal foods. For example, in
Newfoundland, ovenbirds were strongly associated
with deciduous litter patches in an otherwise moss-
covered forest floor, where they were observed hunt-
ing for insects (Thompson et al., 1999), an activity
noted for other insectivorous songbird species by
Willson and Comet (1996) in Alaska. Innes et al.
(1990) found that ground covers influenced inverte-
brate prey and hence numbers of masked shrews
(*Sorex cinereus*) in jack pine plantations in Ontario.
Heather voles (*Phenacomys intermedius*) selected
jack pine forests in northeastern Ontario in relation
to the abundance of low ericaceous shrubs (Naylor and
Bendell, 1983), and small mammals have been more
generally related to several understory structure vari-
ables such as herbaceous plant height and density
(Deuser and Shugart, 1978; Carey and Johnson,
1995). Litter depth, moss cover, woody debris, and
leaf litter type are important variables predicting
salamander presence and abundance (Pough et al.,
1987; DeMaynadier and Hunter, 1995). A major diet
item of red-backed voles (*Clethrionomys gapperi*) is
sporocarps of hypogeous and epigeous fungi (Martell,
1981; Ure and Maser, 1982). These foods are absent in
young stands because of xeric conditions, and may
only develop with sufficient moisture and moss cover
as the forest matures. Lichens are also eaten by voles,
and woodland caribou will seek out mature and older
jack pine and black spruce forests, where ground
lichens are common (e.g. Ahti and Hepburn, 1967;
Schaefer and Pruitt, 1991). Ground covers change
considerably as a result of logging (Carleton, 2000;
Bunnell et al., 1999), and further changes result from

scarification and herbicide application that can alter species composition of ground covers for several decades compared to those following natural disturbances (Brumelis and Carleton, 1991; Ehnes and Shay, 1995; Carleton, 2000).

Canopy cover is an important variable affecting habitat selection by many vertebrate species. For example, marten may use stands with dense canopy cover to avoid avian predators (Hargis and McCullough, 1984). In mixedwood stands, the canopy is rarely fully closed and so light reaches the sub-canopy, and as a result these stands generally have greater vertical structure than either deciduous or conifer stands. A closed canopy results in reduced stand structure, particularly in even-aged conifer plantations because of light exclusion from the forest floor. Sufficiently low light eliminates most plants, including deciduous shrubs and trees, thereby resulting in a fairly simple vertical structure that reduces niche space in the stand. Limited vertical structure excludes many bird species (e.g. De Graaf et al., 1998). Further, minimal light reduces ground covers and flowering plants resulting in little food availability for small mammal species such as red-backed voles, deer mice (*Peromyscus maniculatus*) that are important prey for small boreal predators (Thompson and Colgan, 1991; Hayward et al., 1993).

IFM often results in less complex forest ecosystems than stands that develop following natural processes (Kimball and Hunter, 1990; Moore and Allen, 1999). Ecological literature pertaining to simplification of ecosystems suggests that less 'connected' ecosystems are vulnerable to disruption because of lower redundancy in functional relationships (e.g. Holling, 1992a), and because there is thought to be limited resistance to perturbations and low resilience in such systems (Loreau, 2000; Hector et al., 2001). As a general statement, simple forest ecosystems (i.e. few tree species) support fewer animal or understory plant species than do more diverse forests (e.g. Edenius and Elmberg, 1996; Yamamura, 2002). Although the functional relationship between biodiversity and stability is unclear (e.g. Johnson et al., 1996; Loreau, 2000), especially in complex forested ecosystems, there is evidence that simple ecosystems are vulnerable to rapid loss of function through disturbances such as insect attack, fire, drought, and climate change (Holling, 1992a). Certain intensively managed forest

systems have been susceptible to attacks by herbivores, which, if severe enough, may move the ecosystem to a different and younger state by removing (eating) the high value food patches (Holling, 1992a,b). For example, severe damage by moose and spruce budworm (*Choristoneura fumiferana*) occurred in pre-commercially thinned stands of balsam fir in Newfoundland (Thompson, 1988; Dobesberger, 1998), red deer (*Cervus elaphus*) damaged planted conifers in Britain (Miller et al., 1982), and moose have been a long-standing problem for Scots pine plantations in Sweden (Lavsund, 1981). In these instances, ungulates or insects damaged and killed large numbers of stems over extensive managed areas, compared to lower levels of browsing damage in naturally regenerating forests, and in the Newfoundland case, moose browsing actually resulted in the eventual development of a new forest type (Thompson and Curran, 1993). Strategies to avoid high levels of herbivory have been developed that include increasing species diversity within the stand. For example, Su et al. (1996) recommended increasing non-host content (i.e. hardwood stem density and hence stand complexity) of managed conifer stands in New Brunswick to reduce losses to spruce budworm. Hence, IFM can place some forest ecosystems into a state that is less diverse and less stable than under natural conditions (e.g. Frelich and Lorimer, 1985; Yamamura, 2002), making them potentially vulnerable to rapid disruption by herbivores (DeAngelis et al., 1989; Pimm, 1991; Holling, 1992a). Nevertheless, many forest types within the boreal biome also occur naturally as monocultures (e.g. jack pine, and aspen on uplands, and black spruce on lowlands), suggesting that for certain tree species, high individual density species density is less of a concern than for some others.

An important aspect of possible large-scale, long-term effects of basic silviculture or IFM may be the practice of locating these stands on sites with high productivity, and the associated implicit maintenance of non-riparian habitat for wildlife on poorer or commercially inoperable sites. Just as richer sites produce the best tree growth, in natural forests they may also support the highest densities of various wildlife species populations and high species richness (e.g. Welsh and Loughheed, 1996; Thompson et al., 1999). Decisions taken at the forest landscape scale on the size, amount, and distribution of treated areas might cumulatively

affect wildlife populations across landscapes depending on the amount of land under intensive management. A second important concurrent aspect is the large-scale conversion of upland conifer sites to mixedwoods in the boreal forests, as suggested by Carleton (2000), that is likely to occur even with IFM, which reduces habitat availability to the various species which prefer conifer-dominated habitats.

At broad scales, timber harvesting produces a different landscape pattern from that observed following natural disturbances (Baker, 1995; Gluck and Rempel, 1996; Perera and Baldwin, 2000). The landscape pattern produced by basic post-harvest silviculture over a large area has not been specifically investigated. However, we believe that it would enhance the small-patch pattern already created following logging (Rempel et al., 1997; Perera and Baldwin, 2000), because it modifies further a portion of the logged landscape, in a regular pattern, on the >30% of the area logged which is treated. However, in some situations, Hartley (2002) suggested that intensively managed forest plantations could contribute to local biodiversity, especially in locations that have been deforested, and by improving connectivity among existing forest patches.

4. Models for development of hypothesis of effects on species

We have made general predictions of the effects of different disturbance regimes stand structure and com-

position based on the reviewed studies of vertebrate species responses to post-harvest silviculture (Tables 2 and 3), and changes in landscape composition (Table 4) based on Gluck and Rempel (1996), Rempel et al. (1997), Perera and Baldwin (2000), Elkie and Rempel (2001), to help make inferences about impacts of IFM on various vertebrate species. In order to more explicitly assess the potential cumulative effects of IFM, we developed predictions for a variety of vertebrate species using modelling, based on suitability and amounts of forest types within a landscape.

To generate hypotheses on the effects of IFM on wildlife and to aid in the study design for data collection, we developed an aspatial model of forest change for a managed boreal forest unit (>1200 km²) near Kapuskasing Ontario, based on estimated probabilities (see later and Table 5) that wildlife species would be found (i.e. be observed) in broad forest types and in the various age-classes. The objective of our model was to develop hypotheses based on the long-term (i.e. 30–200 years) predicted effects of IFM on probability of occurrence of the selected wildlife species at a landscape level. The main expectations from the modelling were:

- to predict the relative density and/or presence or absence of each species;
- to make predictions in terms of both long-term mean relative density and variation around this mean;
- to account for continuous changes of the landscape to be modeled (for example, a certain

Table 2

Expected relative effects of three common basic silvicultural practices on stand structures important to vertebrate species, in three stand age-classes in boreal forest, used to develop species/stand probabilities in Appendix A

Variable	Herbicide			Plantation			Scarify and plant		
	Young	Pole	Mature	Young	Pole	Mature	Young	Pole	Mature
Large cavity trees	Few	Few	Few	Few	Few	Few	None	None	None
CWD	High	Medium	Low	High	Medium	Low	Low	Low	Low
Multi-storey	Absent	High	High	Absent	Low	Absent	Absent	Absent	Absent
Deciduous shrubs	Low	High	Medium	Medium	Few	Absent	Low	Few	Absent
Ground cover	Low	Medium	Medium	High	Scant	Low	Low	Low	low
Canopy	Nil	Open	Closed	Nil	Closed	Closed	Nil	closed	closed
Large trees	Few	Nil	Nil	Nil	Few	Nil	Nil	Nil	Nil
Old trees	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil

Based on papers given in 'literature list'.

Table 3

Predicted qualitative relative amounts of stand structural characters important to vertebrate species, in boreal forest stands following logging with and without basic silviculture and IFM, compared to following wildfire, used to develop species/stand probabilities in Appendix A

Variable	Logged only			Logged + basic silviculture			Logged + intensive silviculture			Natural disturbance		
	Young	Pole	Mature	Young	Pole	Mature	Young	Pole	Mature	Young	Pole	Mature
Large cavity trees	Few	Few	Few	None	None	None/few	None	None	None	Medium	Medium	High
CWD	Medium to high	Medium	Low	Scarce	Scarce	Low	Scarce	Scarce	Scarce	High	Medium	Medium
Multi-story ^a	Absent	Medium	High	Absent	Low	Low	Absent	Low	Absent	Low to medium	Medium	High
Deciduous shrubs	High	Medium	Medium	Low	Medium	Low	Low	Low	Low	High	Medium	Low
Ground cover ^b	High	Medium	Medium	Low	Low	Low	Low	Low	Low	High	Medium	High
Canopy	Nil	Open	Closed	Nil	Closed	Closed	Nil	Closed	Closed	Nil to low	Open	Closed
Large trees	Few	None	None	None	None	None	None	None	None	Few	Few	Medium
Old trees	None	None	None	None	None	None	None	None	None	Few	Few	Medium

Based on papers given in 'literature list'.

^a Descriptions shown apply to mixedwoods; values would be less in jack pine (*Pinus banksiana*) or black spruce (*Picea mariana*) stands, except in logged black spruce lowland stands.

^b Ground covers change from mostly litter and woody debris with a high flowering plant richness in younger stands, to more moss with a lower richness of flowering plants as the stand matures.

fraction of the landscape to be disturbed and/or managed every year as opposed to predicting the long-term effects of a one-time change); and

- (d) to compare the species density dynamics for several scenarios of landscape development, such as natural disturbance only, natural disturbance plus logging, natural disturbance plus logging plus IFM.

The selected wildlife species were based on our literature review and suggested indicator species in

boreal forests of Ontario (McLaren et al., 1998). Species are listed in Appendix A, along with estimated probabilities of occurrence by forest type and post-harvest treatment. Sufficient information exists about these species to predict relative stand and population level effects of basic silviculture and IFM. The probabilities of occurrence in forest types and ages were based on information previously published for the species selected (Table 5) and the expected responses to the qualitative habitat variables shown in Tables 2–4.

Table 4

Predicted relative landscape structural characteristics, in mature Ontario forests following logging, with and without basic silviculture, compared to a natural-origin landscape, used to develop species/stand probabilities in Appendix A

Variable	Logged only	Logged + basic silviculture	Logged + intensive silviculture	Natural disturbance
Edge	High	High	High	Low
Patch size	Small	Small	Small	Medium-large
%Conifer stands	Low	Medium	Medium	Medium-high
%Mixed stands	Medium	High	Low	Medium
%Deciduous stands	High	Medium	Low	Low
%Old forest	Low	Low	Low	High ^a
Interior forest	Low	Low	Low	High ^a

Based on: Gluck and Rempel (1996), Rempel et al. (1997), Perera and Baldwin (2000), Elkie and Rempel (2001).

^a Under an natural disturbance regime, the amount of old forest in a given area will vary over long time scales.

Table 5

Published studies used to develop species/stand probabilities of occurrence for boreal forests in Ontario, Canada, presented in Appendix A

Vertebrate group	Published studies
Birds	Ersine (1977), Temple et al. (1979), Cadman et al. (1987), Hayward et al. (1993), Welsh and Loughheed (1996), De Graaf et al. (1998), McLaren et al. (1998), Imbeau et al. (1999), Thompson et al. (1999), Setterington et al. (2000), Drapeau et al. (2000), Kirk and Hobson (2001)
Mammals	Banfield (1974), Stelfox et al. (1976), Martell and Radvanyi (1977), Naylor and Bendell (1983), Martell (1983), Clough (1987), Nordyke and Buskirk (1991), Thompson (1994), Thompson and Curran (1995), Sullivan et al. (1997), McLaren et al. (1998), Potvin et al. (2000)
Amphibians	Pough et al. (1987), DeMaynadier and Hunter (1995, 1997, 2000), McLaren et al. (1998), Welsh and Droegge (2001)

based on a workshop attended by boreal species experts, held to select indicator species for Ontario (see McLaren et al., 1998), and our collective opinions based on an a cumulative 65 years of working in boreal forests. Forest change in time and harvest was based on outputs from the aspatial 'Ontario Strategic Forest Management Model' (SFMM) (including forest composition and harvest allocations), and vegetation transition matrices from (Carleton, 2000). SFMM is an analytical tool used to forecast timber supply and develop harvest allocations on a management unit basis. Following are the rules applied to our aspatial model.

1. The model simulated overall relative population density of a given wildlife species (Appendix A) in 'available' forest (i.e. available for management) in the management unit. Total area of available forests in the unit was 1,256,000 ha. The area size was constant throughout all simulation steps, i.e. fluctuations due to conversion of reserve forest into available forest, afforestation, and natural disturbances were ignored.
2. The starting age/forest type distribution was taken from the SFMM output for year 2000 for the Gordon Cosens Forest (obtained from Tembec Inc., Kapuskasing, Ontario). Forest types used in SFMM were re-grouped (Table 6) into a vegetation transition matrix for those types used by Carleton (2000), for which we had probabilistic transitions.
3. The length of one simulation step was 10 years, and the total simulation time was 200 years.
4. The model did not simulate vegetation changes that may have occurred as the vegetation age increased. That is, once the harvested area was

'regenerated' as a certain forest type, it remained in the same type for the entire simulation period, or until harvested again.

5. Regeneration of the harvested areas was performed using three matrices: natural regeneration (Carleton, 2000) (Table 7), regeneration with basic silviculture (Carleton, 2000) (Table 8), and regeneration with IFM (diagonal matrix that assumed the forest regenerated to the same forest type that was there prior to harvesting).
6. Harvest age was set to 80 years and greater; that is, all forest stands that were >80 years old were considered available for harvesting within a given decade.
7. Harvest rate was set at 10% of the total available forest per decade, and was kept constant throughout all simulation steps. This amounted to about 125,000 ha per decade. The harvest rate could be increased slightly, but could not exceed 11.1% in a decade (the actual harvest area recommended by

Table 6

Grouping of forest types from the Ontario strategic forest management model (SFMM) output to forest types as used by Carleton (2000)

Forest types used in the SFMM model	Forest types used by (Carleton, 2000)
Upland mixed	Mixed hardwood–softwood
Upland depleted	–
Upland conifer	Mixed softwood
Lowland spruce	Black spruce ^a
Lowland swamp	–
Lowland transition	–
Jack pine	Jack pine
Hardwood	Hardwood

^a Black spruce (*Picea mariana*), jack pine (*Pinus banksiana*).

Table 7

Matrix of expected forest types following logging in original forests and natural regeneration, based on Carleton (2000, Fig. 10.9a)

Original forest type	Resulting forest type after logging – no basic silviculture				
	M	MS	SB	PJ	H
Mixedwood (M)	0.5	0.13	0.03	0.05	0.29
Mixed softwood (MS)	0.42	0.29	0.06	0.06	0.17
Black spruce ^a (SB)	0.28	0.42	0.14	0.02	0.14
Jack pine (PJ)	0.46	0.15	0	0.15	0.24
Hardwoods (H)	0.52	0.1	0	0.06	0.32

^a Black spruce (*Picea mariana*), jack pine (*Pinus banksiana*).

SFMM for the area was 14,000 ha per year, which is about 11.1% over a decade).

8. The model assumed a 'proportional' harvesting scenario, that is, allocation of the area to be harvested, within a given decade to each forest type, was proportional to the area occupied by the forest of this type in ages >80 years. The harvesting scenario changed slightly after the first rotation, so that areas under IFM were considered 'primary' targets for harvesting.
9. Regeneration scenarios were defined as various percentage combinations of natural regeneration, regeneration with basic silviculture, and regeneration with IFM. Regeneration scenarios remained constant throughout all simulation steps. The allocation of regeneration management types to harvested forest types was as follows:
 - (a) First, IFM was allocated to three forest types: MS (mixed softwood), JP (jack pine), and BS (black spruce). If the area to be treated under IFM was less than the area harvested in these three forest types, then IFM was proportionally allocated to the three types. If the area to be treated under IFM exceeded the harvested

area in the three forest types, then the latter area was assigned to IFM, and the remaining area to be treated under IFM was proportionally assigned to the remaining two forest types (i.e. mixedwood and hardwood).

- (b) Basic silviculture was applied proportionally to the area remaining after applying IFM; natural regeneration was applied to the area remained after applying IFM and basic silviculture (see no. 12 later for scenario areas treated by basic silviculture and IFM).
10. Relative density of each wildlife species was calculated at every step by multiplying the wildlife suitability values (Appendix A) by the area fraction occupied by a respective forest type/age/management type. Results were summed over the entire available forest area for the species considered.
11. The model(s) did not account for any interactions between species, such as resource competition or predator-prey relationships.
12. The model was run for three scenarios: 100% natural regeneration following logging, 60% natural regeneration plus 40% basic silviculture

Table 8

Matrix of expected forest types following logging in original forests and basic silviculture, based on Carleton (2000, Fig. 10.9b)

Original forest type	Resulting forest type after logging – with basic silviculture				
	M	MS	SB	PJ	H
Mixedwood (M)	0.42	0.21	0.04	0.11	0.22
Mixed softwood (MS)	0.32	0.18	0.05	0.27	0.18
Black spruce ^a (SB)	0.37	0.3	0.11	0.07	0.15
Jack pine (PJ)	0.28	0.17	0	0.44	0.11
Hardwoods (H)	0.44	0.19	0.06	0.12	0.19

^a Black spruce (*Picea mariana*), jack pine (*Pinus banksiana*).

Table 9

Modeled output of predicted differences in relative population density (percentage of density for 100% natural regeneration scenario) between the following regeneration scenarios: scenario 1, 100% natural regeneration; scenario 2, 60% natural regeneration, 40% basic silviculture; scenario 3, 60% natural regeneration, 40% IFM

Species	Difference in year 100 (percentage change in relative density vs. year 0)			Difference in year 200 (percentage change in relative density vs. year 0)			Mean percentage difference at 200 year mean vs. initial value at year 0	
	Scenario 1	Scenario 2	Scenario 3	Scenario 1	Scenario 2	Scenario 3	Scenario 2	Scenario 3
Moose (<i>Alces alces</i>)	39.7	27.1	8	53.6	36	11.5	-9.8	-22.9
Marten (<i>Martes americana</i>)	-18.1	-23.6	-23.8	-19.7	-25	-24.4	-4.4	-3.9
Lynx (<i>Lynx canadensis</i>)	25.6	17	-0.9	33.7	22.3	1.3	-7.2	-20.2
Snowshoe hare (<i>Lepus americana</i>)	25.6	15.9	-0.9	33.7	21.2	1.3	-7.9	-20.2
Red-backed vole (<i>Clethrionomys gapperi</i>)	-24.6	-29.6	-33.6	-29	-33	-35.5	-4.5	-7.1
Red crossbill (<i>Loxia curvirostra</i>)	-47.5	-48.6	-26.2	-57.2	-58.1	-33.5	-1.5	24.7
Cape May warbler (<i>Dendroica tigrina</i>)	-44.5	-43.9	-27.7	-53.1	-52.4	-33.6	0.4	19.2
Tennessee warbler (<i>Vermivora peregrina</i>)	-40.6	-39.8	-20.6	-50.8	-49	-26.8	1	24.2
Hairy woodpecker (<i>Picoides villosus</i>)	-4.6	-18.7	-21.1	-0.3	-15.6	-18.4	-11.4	-13.2
Black-backed woodpecker (<i>Picoides arcticus</i>)	-36	-32.7	-22	-44.7	-39.8	-24.4	3.6	15.9
Yellow-bellied flycatcher (<i>Empidonax flaviventris</i>)	-30.2	-27	-9.9	-39.9	-36.3	-14.5	3.1	22.6
Red-breasted nuthatch (<i>Sitta canadensis</i>)	-28.8	-33.8	-30.2	-33.9	-38.3	-33.2	-4.6	-0.5
Salamanders spp.	-1	-10.2	-17.7	3.3	-7.2	-16.3	-8.1	-14.7

See text for a description of how the scenarios were applied.

following logging, and 60% natural regeneration with 40% IFM after logging.

4.1. Results of aspatial modelling

Our results (Table 9) are relative and not absolute, and so represent hypothetical predictions. Because of the coarse resolution used in the model parameters, there is potential for error in the parameter estimates and thus in the predictions. Eventual tests of these predictions (which are de facto hypotheses) are feasible using empirical data on relative densities among treatments for each of the various species. Clear differences among the regeneration scenarios for forest recovery and change were suggested by the model (Fig. 2). Only with 40% IFM was a decline in black spruce curtailed over time, while under fully natural regeneration or with 40% basic silviculture, there was a predicted substantial increase in mixedwoods and hardwoods. A decline in black spruce has been predicted elsewhere for Ontario as a result of timber harvesting and known regeneration patterns (Hearn-den et al., 1992; Baker et al., 1996).

For wildlife, the results of the aspatial models suggested that effects on most species can be expected,

but that these would differ among treatments and individual species (Fig. 3a–m). Several species were predicted to respond positively to IFM (and basic silviculture), compared to allowing solely natural regeneration to occur following harvesting, with the largest effects predicted for red crossbill, Tennessee warbler, Cape May warbler, and yellow-bellied flycatcher. Negative impacts of IFM, compared to natural regeneration, were predicted for moose, lynx (*Lynx canadensis*), snowshoe hare (*Lepus americana*), hairy woodpecker (*Picoides villosus*), and yellow-spotted and blue-spotted salamanders (*Ambystoma maculatum* and *A. laterale*). Relatively minor negative effects were predicted for red-breasted nuthatch (despite our expectation of fewer cavity trees) and marten. The model predicted generally positive effects of logging, regardless of the regeneration scenario, for moose, lynx, and snowshoe hare. These effects might be expected under a reduced rotation age harvest that would result in an increase of younger habitats across a landscape, as well as an increase in mixedwoods. Over the longer-term, negative impacts of forest harvesting were suggested for marten, red-backed vole, red crossbill, Tennessee warbler, and Cape May warbler. Further, in the case of several species no asymptote was apparent even by the

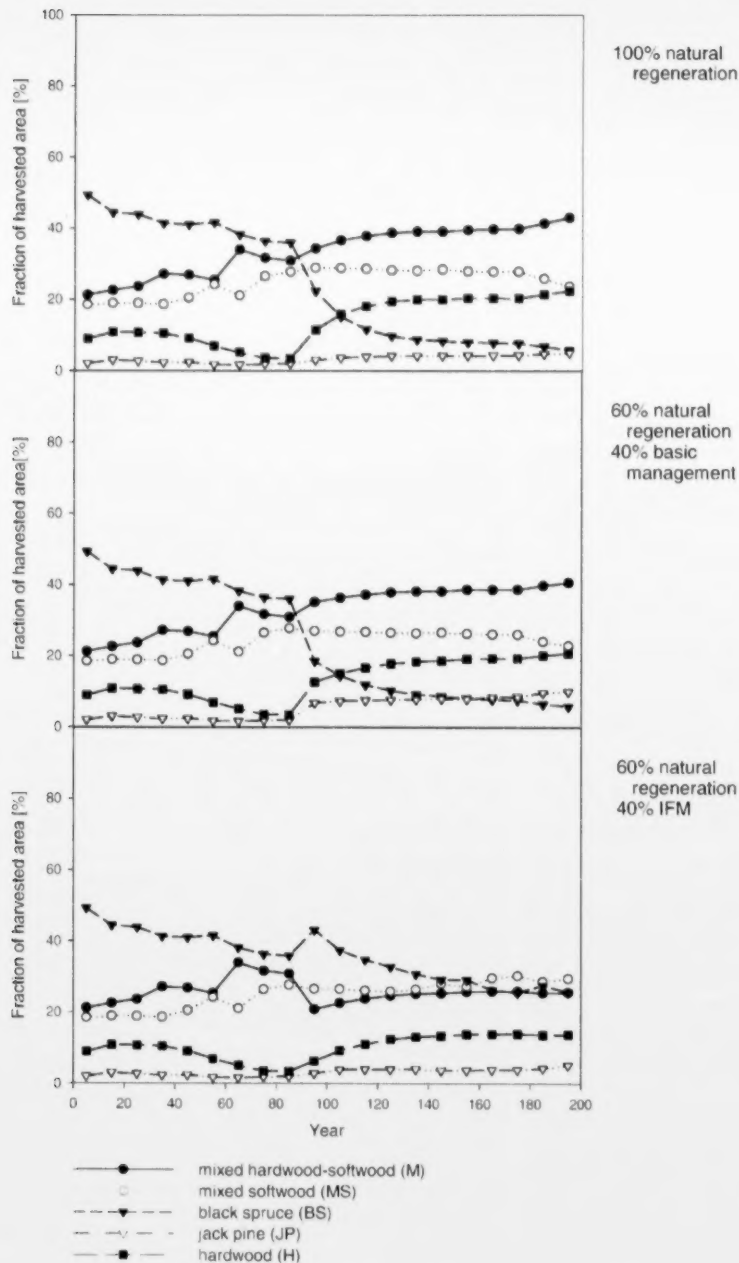


Fig. 2. Changes in main forest types as predicted by aspatial modelling.

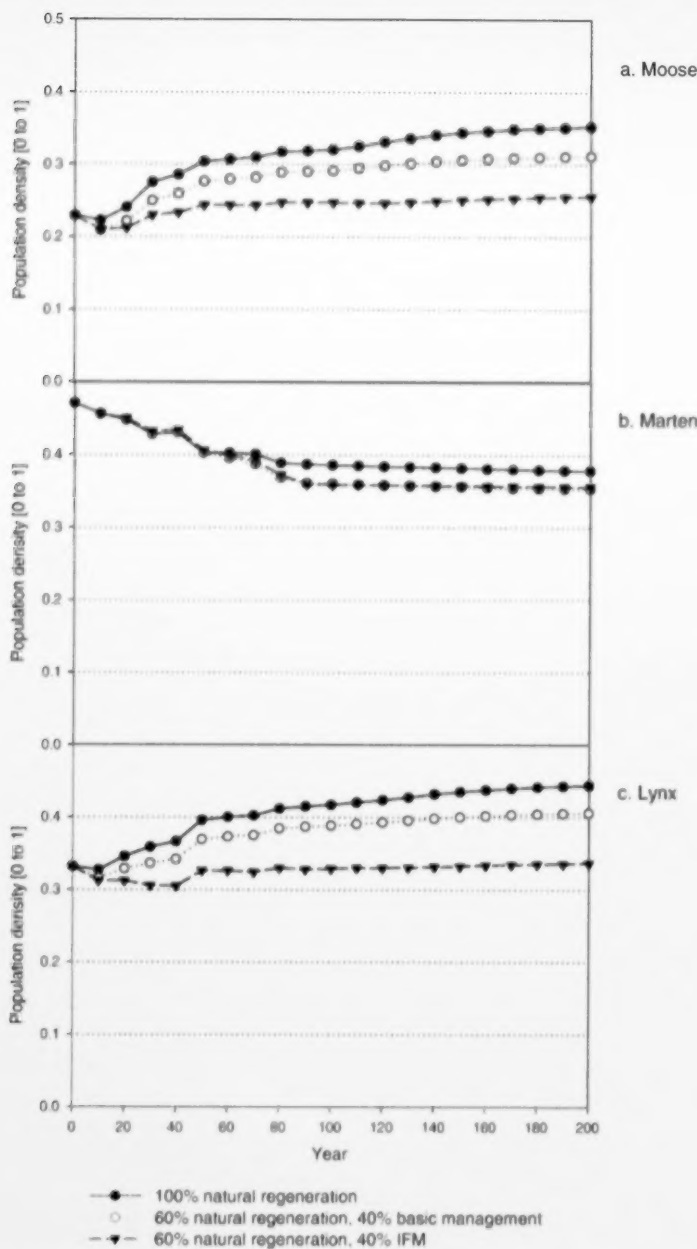


Fig. 3. Predicted individual species responses from aspatial modelling of three forest management scenarios on a boreal forest management unit near Kapuskasing, Ontario, Canada: (a) moose (*Alces alces*); (b) marten (*Martes americana*); (c) lynx (*Lynx canadensis*); (d) snowshoe hare (*Lepus americanus*); (e) red-backed vole (*Clethrionomys gapperi*); (f) red crossbill (*Loxia curvirostra*); (g) Cape May warbler (*Dendroica tigrina*); (h) Tennessee warbler (*Vermivora peregrina*); (i) hairy woodpecker (*Picoides villosus*); (j) black-backed woodpecker (*Picoides arcticus*); (k) yellow-bellied flycatcher (*Empidonax flaviventris*); (l) red-breasted nuthatch (*Sitta canadensis*); (m) salamanders (*Ambystoma maculatum* and *A. laterale*).

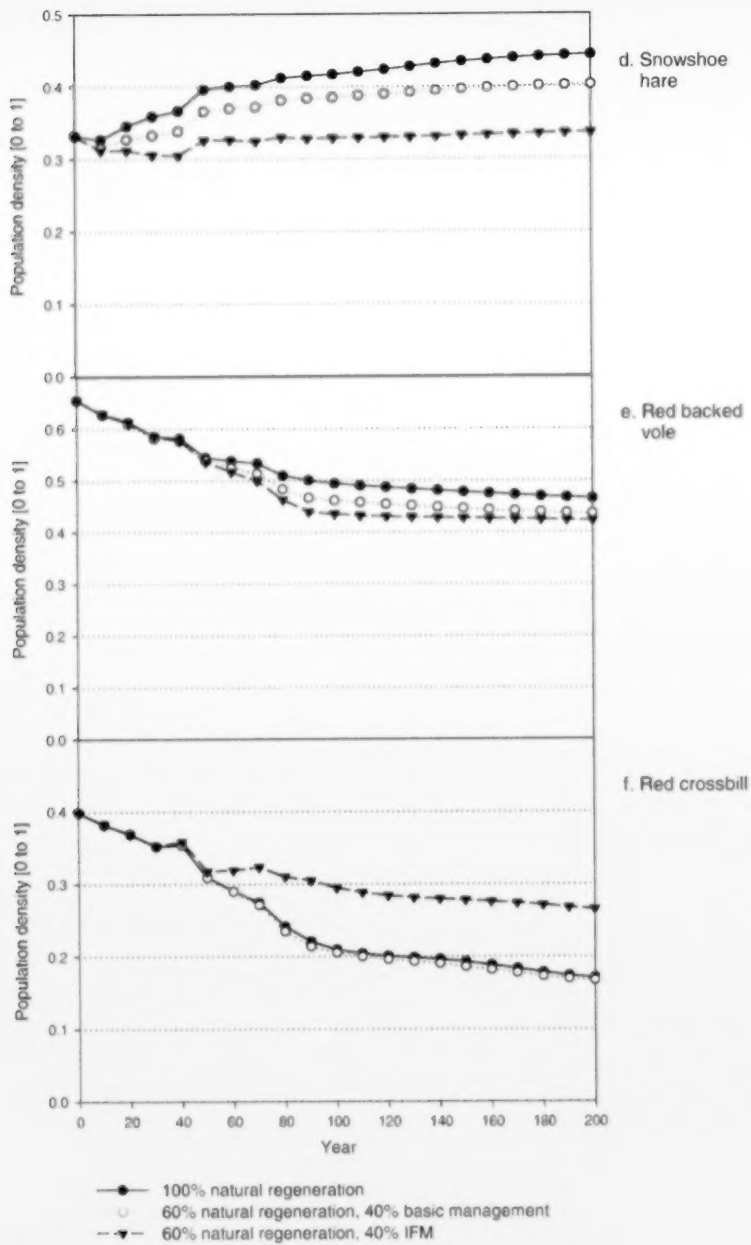


Fig. 3. (Continued).

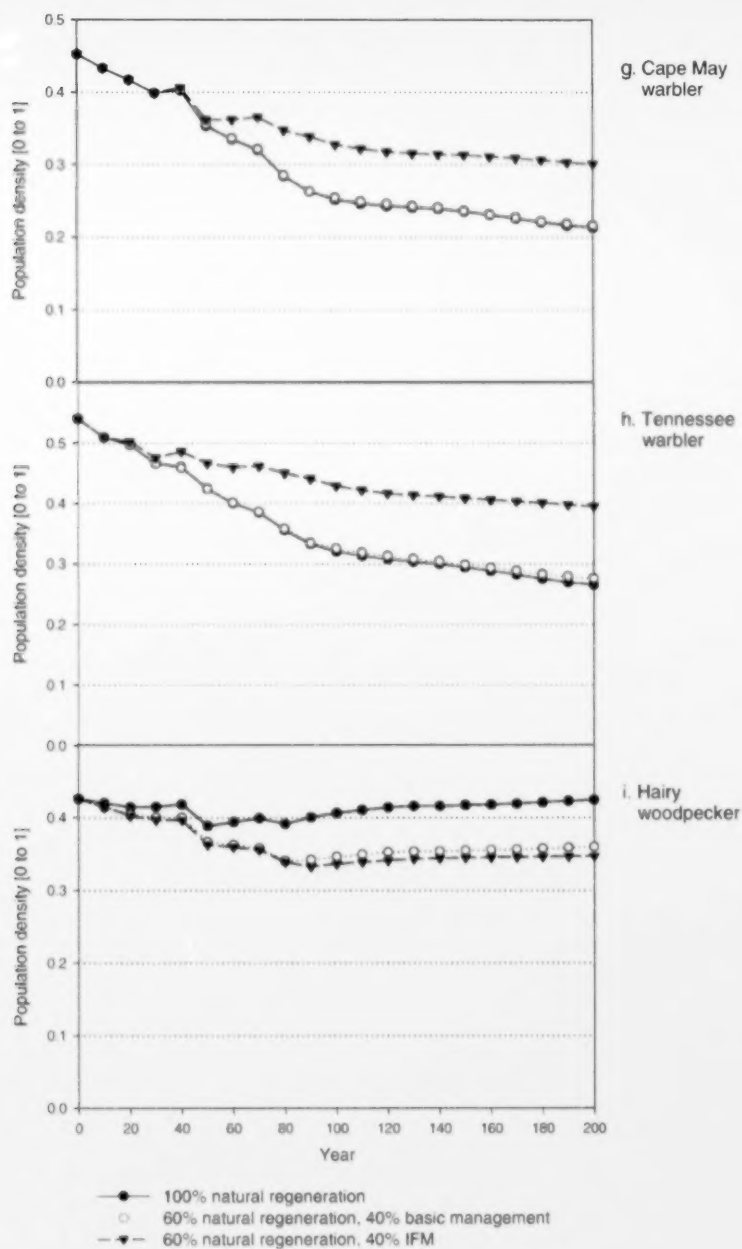


Fig. 3. (Continued).

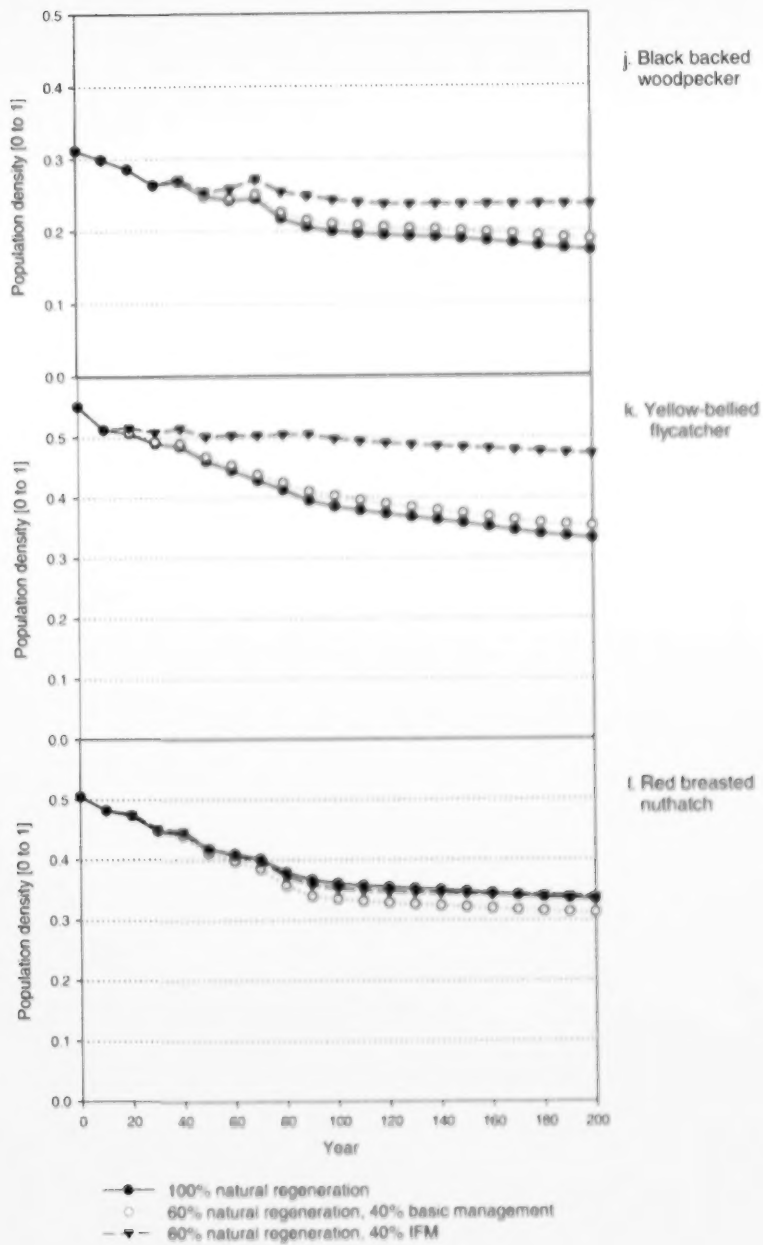


Fig. 3. (Continued).

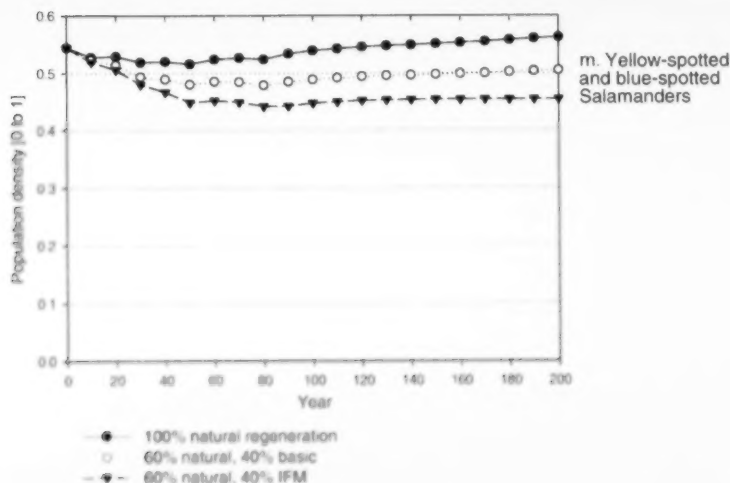


Fig. 3. (Continued).

second rotation suggesting that potential impacts were cumulative over the long-term.

4.2. Summary of predicted effects of basic and intensive silviculture

Based on the aspatial model, we expect that some of the selected indicator species will be affected positively and others negatively at stand and landscape scales, by basic silviculture and IFM (Table 10, Fig. 3a–m). Stand level effects will occur as animals respond to structures created or destroyed by silviculture, but the effects at the population level for any species is dependent on the total amount of area treated within a given landscape. Effects will be most evident on species with large home ranges, while for species with small home ranges, population effects may not be observed until high portions of a given landscape are under basic silviculture or IFM.

Among our selected species, some are predicted to be positively affected by IFM, as a result of increased conifer and mixed forests compared to stands developing following harvesting as the sole silvicultural treatment (Fig. 3a–m) (e.g. red crossbill). Other species will respond negatively to increased IFM we suspect, because of the loss of stand structures or change in forest age (e.g. moose). Although considerable

variability exists among stands, in general, stand level effects should be relatively straight forward to predict based on linear response to the structural changes suggested in Tables 2 and 3. Spatial landscape (or management unit response) might be predictable using several models, for example, a linear population response, suggested by Andren (1994) and others (e.g. Voigt et al., 2000) for landscapes above certain thresholds, e.g. <70% change; and metapopulation models that generally predict logarithmic asymptotic responses to habitat change based on dispersal distance capacity and patch sizes (Hanski et al., 1996).

Based on our assumptions (Tables 2–4), we do not believe that an additional impact of IFM would be substantial in the short-term (50 years), beyond the impacts of basic silvicultural treatments following logging. Increased effects were predicted to occur during and beyond the second rotation, especially for species requiring large expanses of older conifer. Further, the models suggested that logging followed by any type of treatment has long-term effects on habitat quality (positive for some species and negative for others). So, the immediate concern is not just the effect of additional IFM, but also the longer-term effects of all silvicultural treatments. Such effects are likely to include the relative availability of the various

Table 10

Summary predicted effects of IFM silviculture on selected species at stand (>20 ha) and landscape scales (e.g. 500 km²), based on aspatial modelling

Species ^a	Predicted response vs. natural regeneration	Expected effect of IFM silviculture	Scale of effect
Marten	Negative	Reduced CWD and snags and less old forest	Landscape
Lynx	Negative	Reduced deciduous shrubs	Landscape
Snowshoe hare	Negative	Reduced hare habitat	Landscape
Red-backed vole	Negative	Early crown closure offset by reduced CWD and reduced ground covers	Stand
Moose	Negative	Reduced deciduous herbs	Landscape
Red crossbill	Positive	Increased Pw, Sw ^b and other conifers	Landscape
Cape May warbler	Positive	Increased mixedwood and conifer	Stand
Tennessee warbler	Positive	Increased conifer	Stand
Hairy and downy woodpeckers	Negative	Loss of snags (and CWD)	Stand and landscape
Black-backed and three-toed woodpeckers	Positive	Early crown closure and increased conifer	Stand and landscape
Yellow-bellied flycatcher	Positive	Increased white spruce	Stand
Red-breasted nuthatch	No effect	–	Stand
Amphibians (all)	Negative	Limited CWD and reduced ground covers	Stand

Magnitude of any effect would depend on the amount of basic silviculture within a landscape, and thresholds likely exist.

^a See Table 9 for Latin nomenclature.

^b Pw: white pine (*Pinus strobus*); Sw: white spruce (*Picea glauca*).

stand types, and changes in stand and landscape structure. An uncertainty is the assumed structural difference between naturally disturbed stands and logged stands, particularly because little individual ecosystem information on wildlife species responses is available. There are few empirical comparisons of vegetation structure and composition, and the accompanying wildlife response in forests originating from natural disturbances and logging, to reduce the uncertainty of this conclusion.

A subsequent question pertains to the thresholds of spatial and temporal effects of basic silviculture and IFM on animal populations. For example, we have identified what some of the effects might be for some species (Table 10), but the magnitude of these effects (population decline and density differences) may vary among the species at different thresholds. That is, the measurable impacts on marten, for example, may not be detectable until 50% of the forest is managed, whereas, perhaps only 20% might be needed to observe a measurable impact on lynx.

In a sense, these basic and IFM silvicultural treatment effects may be analogous to fragmentation effects, with fragments of preferred habitat for a given species represented by, at some level, the remaining

naturally-regenerating stands (or naturally disturbed stands). For example, Andren (1994) discussed fragmentation effects, and predicted that non-linear declines for species would occur if there was 30% or less of a particular habitat remaining. Thompson and Harestad (1994) predicted that effects of forest management on marten would not be seen until at least 30% of the mature forest landscape was altered, based on the correlation between animal density and habitat area (Connor et al., 2000). Although we do not advocate that fragmentation can occur in continuous forests, the distribution of species' habitats across a landscape does change in time and therefore affects populations. For example, the distribution of old conifer-dominated habitat on the landscape may decline as a result of reduced rotation age in stands of basic silviculture and IFM origin. The reduction of continuous old forest habitats would produce landscape-scale effects (i.e. long-term population declines among certain species) (e.g. Thompson et al., 1999; Kirk and Hobson, 2001). For example, larger patches of habitat are more important to maintaining populations in time than are multiple small patches (Connor et al., 2000). The ultimate effects of IFM on wildlife will depend on the total area of habitat affected, its

distribution on the landscape, individual patch sizes, and the individual species, with some species positively affected and others negatively affected. The important question is whether the negative effects result in sufficiently reducing the local population of a species to a sufficiently low level so that it becomes a concern.

Appendix A

Proposed probabilities for species habitat use for forest types following: logging with natural regeneration/logging with basic silviculture/logging with intensive silviculture, in Ontario boreal forests. Where a single value is given, that value is uniform for the three treatments (see text for derivation methods) (Pj: jack pine [*Pinus banksiana*], Sb: black spruce [*Picea mariana*], MS: mixed softwoods, M: mixedwoods, H: hardwoods) (see Table 9 for Latin nomenclature for vertebrate species).

	5–10 years	10–30 years	30–50 years	50–80 years	>80 years
Moose					
Pj	0.3/0.1/0.1	0.2/0.1/0.1	0.1	0.1	0.1
Sb	0.3/0.1/0.1	0.2/0.1/0.1	0.1	0.1	0.1
MS	0.3/0.1/0.1	0.2/0.2/0.2	0.1	0.1	0.1
M	0.6/0.1/0.1	1.0/0.6/0.5	0.5/0.5/0.4	0.3	0.2
H	0.4/0.1/0.1	0.7/0.5/0.4	0.4	0.2	0.1
Marten					
Pj	0	0.2	0.2	0.4/0.3/0.3	0.6/0.4/0.4
Sb	0	0.2	0.3	0.6/0.4/0.4	0.6/0.5/0.4
MS	0	0.2	0.3	0.6/0.4/0.4	0.7/0.5/0.4
M	0	0.1	0.4	0.7/0.4/0.3	0.9/0.6/0.5
H	0	0.1	0.1	0.4	0.4
Lynx					
Pj	0.3/0.1/0	0.4/0.3/0.1	0.3	0.2	0.1
Sb	0.3/0.1/0	0.4/0.3/1	0.3	0.2	0.1
MS	0.3/0.1/0	0.4/0.3/0.1	0.3	0.2	0.2
M	0.5/0.1/0.1	0.9/0.6/0.4	0.9/0.7/0.5	0.5	0.4
H	0.3/0.1/0.1	0.5/0.4/0.4	0.4	0.2	0.1
Snowshoe hare					
Pj	0.3/0.1/0	0.4/0.2/0.1	0.3	0.2	0.1
Sb	0.3/0.1/0	0.4/0.2/0.1	0.3	0.2	0.1
MS	0.3/0.1/0	0.4/0.2/0.1	0.3	0.2	0.2
M	0.5/0.1/0	0.9/0.7/0.5	0.9/0.7/0.5	0.5	0.4
H	0.3/0.1/0.1	0.5/0.4/0.4	0.4	0.2	0.1
Red-backed vole					
Pj	0	0.1	0.2	0.5/0.3/0.2	0.7/0.5/0.3
Sb	0.1	0.3/0.3/0.2	0.6/0.6/0.3	0.8/0.6/0.4	0.9/0.7/0.5
MS	0.1	0.3/0.3/0.2	0.5/0.5/0.3	0.8/0.6/0.4	1.0/0.8/0.6

Appendix A. (Continued)

	5–10 years	10–30 years	30–50 years	50–80 years	>80 years
M	0	0.2/0.1/0.1	0.4/0.4/0.3	0.8/0.6/0.4	1.0/0.8/0.6
H	0	0	0.1	0.3	0.3
Red crossbill					
Pj	0	0	0	0	0
Sb	0	0	0.2	0.8/0.9/1.0	0.9/1.0/1.0
MS	0	0	0.1	0.5/0.7/0.8	0.7/0.8/0.9
M	0	0	0	0.3	0.5
H	0	0	0	0	0
Cape May warbler					
Pj	0	0	0	0	0
Sb	0	0	0.3	0.8/0.9/1.0	1
MS	0	0	0.2	0.6/0.7/0.8	0.8/0.9/0.9
M	0	0	0.1	0.4	0.6/0.6/0.8
H	0	0	0	0	0.1
Tennessee warbler					
Pj	0	0.1	0.3	0.3	0.5
Sb	0	0.3	0.6/0.6/0.8	0.9/1.0/1.0	1
MS	0	0.2	0.4/0.4/0.5	0.7/0.8/0.9	0.9
M	0	0.1	0.2	0.4	0.4
H	0	0	0	0	0
Hairy woodpecker					
Pj	0	0	0.1	0.3	0.3
Sb	0	0	0.1	0.4/0.3/0.3	0.5/0.4/0.3
MS	0	0.1	0.3/0.2/0.2	0.5/0.3/0.3	0.6/0.4/0.3
M	0.3/0/0	0.3/0.1/0.1	0.2/0.1/0.1	0.6/0.3/0.2	0.8/0.6/0.5
H	0.3/0.2/0.1	0.3/0.2/0.1	0.2/0.1/0.1	0.6/0.3/0.2	0.9/0.8/0.7
Black-backed woodpecker					
Pj	0	0	0.1	0.5/0.6/0.7	0.7
Sb	0	0	0.1/0.2/0.2	0.3/0.4/0.5	0.6/0.7/0.7
MS	0	0	0.2	0.5/0.6/0.7	0.8
M	0	0	0.1	0.2	0.4
H	0	0	0	0	0
Yellow-bellied flycatcher					
Pj	0	0	0.1	0.2	0.2
Sb	0	0.5/0.6/0.6	0.6/0.7/0.7	0.8/0.9/1.0	0.8/0.9/1.0
MS	0	0.5/0.6/0.6	0.6/0.7/0.8	0.8/0.9/1.0	0.7/0.9/1.0
M	0	0.3/0.4/0.4	0.4/0.5/0.6	0.5/0.6/0.7	0.5/0.7/0.7
H	0	0	0	0	0
Red-breasted nuthatch					
Pj	0	0.1	0.2	0.4/0.3/0.2	0.5/0.4/0.3
Sb	0	0.2	0.5/0.4/0.3	0.7/0.6/0.5	0.8/0.6/0.6

Appendix A. (Continued)

	5–10 years	10–30 years	30–50 years	50–80 years	>80 years
MS	0	0.2	0.4/0.3/0.3	0.6/0.4/0.4	0.7/0.5/0.5
M	0	0.1	0.3/0.2/0.2	0.5/0.4/0.4	0.7/0.5/0.5
H	0	0.1	0.2	0.2	0.2
Salamanders					
Pj	0	0	0.2	0.3	0.5
Sb	0.2/0/0	0.3/0.1/0	0.5/0.4/0.2	0.5	0.5
MS	0.2/0/0	0.3/0.1/0	0.5/0.4/0.2	0.5/0.5/0.4	0.5/0.5/0.4
M	0.2/0.1/0	0.5/0.2/0.2	0.6/0.5/0.3	0.7/0.6/0.5	0.9/0.8/0.5
H	0.2/0.1/0	0.5/0.2/0.2	0.7/0.6/0.4	0.7/0.6/0.6	0.9/0.7/0.6
Boreal owl					
Pj	0	0.2	0.2	4/0.3/0.3	7/0.4/0.4
Sb	0	0.2	0.3	6/0.4/0.4	9/0.6/0.4
MS	0	0.2	0.3	6/0.4/0.4	9/0.6/0.4
M	0	0.1	0.4	6/0.4/0.3	9/0.6/0.5
H	0	0.1	0.1	0.4	0.4

References

- Ahti, T., Hepburn, R.L., 1967. Preliminary studies on woodland caribou range, especially on lichen stands, in Ontario. Ontario Department of Lands and Forest Research Report (Wildlife), vol. 74, 134 pp.
- Andren, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355–366.
- Angelstam, P., 1990. Factors determining the composition and persistence of local woodpecker assemblages in taiga forest in Sweden—a case for landscape ecological studies. In: Carlson, A., Aulén, G. (Eds.), *Conservation and Management of Woodpecker Populations*. Department of Wildlife Ecology Report 17, Swedish University of Agricultural Science, Uppsala, pp. 147–164.
- Angelstam, P., 1992. Changes in forest landscapes and bird conservation in northern Europe. *Acta Int. Ornith. Congr.* 20, 2292–2297.
- Aubry, K.B., 2000. Amphibians in managed, second-growth Douglas-fir forests. *J. Wildl. Manage.* 64, 1041–1052.
- Baguette, M., Deceuninck, B., Mueller, Y., 1994. Effect of spruce afforestation on bird community dynamics in a native broad-leaved forest area. *Acta Oecol.* 15, 275–288.
- Baker, W.L., 1995. Long-term response of disturbance landscapes to human intervention and global change. *Landsc. Ecol.* 10, 143–159.
- Baker, J.A., Clark, T., Thompson, I.D., 1996. Boreal mixedwoods as wildlife habitat: observations, questions, and concerns. In: Smith, C.R., Crook, G.W. (Eds.), *Advancing Boreal Mixed-wood Management in Ontario*. Natural Resources Canada and Ontario Ministry of Natural Resources, Sault Ste. Marie, Ont., Canada, Fo18-40, pp. 41–52.
- Banfield, A.W.F., 1974. *The Mammals of Canada*. National Museum of Natural Sciences and University of Toronto Press, Toronto, Ont., Canada, p. 438.
- Barber, D.R., Martin, T.E., Melchior, M.A., Thill, R.E., Wigley, T.B., 2001. Nesting success of birds in different silvicultural treatments in southeastern US pine forests. *Conserv. Biol.* 15, 196–207.
- Bell, F.W., Pitt, D.G., Irvine, M., Parker, W.C., Buse, L.J., Stocker, N., Towill, W.D., Chen, H., Pinto, F., Brown, K., DeYoe, D., McDonough, T., Smith, G., Weber, M., 2000. *Intensive Forest Management in Ontario: Summary of a 1999 Science Workshop*. Science and Development Transfer Series 003, Ontario Ministry of Natural Resources, Sault Ste. Marie, Ont., Canada, 86 pp.
- Bennett, S.H., Gibbons, J.W., Glanville, J., 1980. Terrestrial activity, abundance, and diversity of amphibians in differently managed forest types. *Am. Midl. Nat.* 103, 412–416.
- Bowman, J.C., Sleep, D., Forbes, G.J., Edwards, M., 2000. The association of small mammals with coarse woody debris at log and stand scales. *For. Ecol. Manage.* 129, 119–124.
- Brawn, J.D., Robinson, S.K., Thompson, F.R., 2001. The role of disturbance in the ecology and conservation of birds. *Ann. Rev. Ecol. Syst.* 32, 251–276.
- Brumelis, G., Carleton, T.J., 1991. The vegetation of post-logged black spruce lowlands in central Canada. II. Understory plant cover. *J. Appl. Ecol.* 26, 321–339.
- Bunnell, F.L., Kremser, L.L., Wind, E., 1999. Managing to sustain vertebrate richness in forests of the Pacific Northwest: relationships within stands. *Environ. Rev.* 7, 97–146.

- Buskirk, S.W., Forrest, S.C., Raphael, M.G., Harlow, H.J., 1989. Winter resting site ecology of marten in the central Rocky Mountains. *J. Wildl. Manage.* 53, 191–196.
- Cadman, M.D., Eagles, P.F.J., Helleiner, F.M., 1987. Atlas of the breeding birds of Ontario. University of Waterloo Press, Waterloo, p. 617.
- Carey, A.B., 2000. Effects of new forest management strategies on squirrel populations. *Ecol. Appl.* 10, 248–257.
- Carey, J.B., Johnson, M.L., 1995. Small mammals in managed, naturally young- and old-growth forests. *Ecol. Appl.* 5, 336–352.
- Carleton, T.J., 2000. Vegetation responses to the managed forest landscape of central and northern Ontario. In: Perera, A.H., Euler, D.L., Thompson, I.D. (Eds.), *Ecology of a Managed Terrestrial Landscape: Patterns and Processes of Forest Landscapes in Ontario*. UBC Press, Vancouver, BC, Canada, pp. 178–197.
- Christian, D.P., Hoffman, W., Hanowski, J.M., Niemi, G.J., Beyea, J., 1998. Bird and mammal diversity on woody biomass plantations in North America. *Biomass Bioenergy* 14, 395–402.
- Chritton, C.A., 1988. Effects of thinning a loblolly pine plantation on nongame bird populations in east Texas. M.Sc. Thesis, Austin State University, Austin, TX.
- Clough, G.C., 1987. Relations of small mammals to forest management in northern Maine. *Can. Field Nat.* 101, 40–48.
- Clout, M.N., Gaze, P.D., 1984. Effects of plantation forestry on birds in New Zealand. *J. Appl. Ecol.* 21, 795–815.
- Connor, E.F., Courtney, A.C., Yoder, J.M., 2000. Individuals-area relationships: the relationship between animal population density and area. *Ecology* 81, 734–748.
- DeAngelis, D.L., Mulholland, P.J., Palumbo, A.V., Steinman, A.D., Huston, M.A., Elwood, J.W., 1989. Nutrient dynamics and food-web stability. *Ann. Rev. Ecol. Syst.* 20, 71–95.
- De Bellefeuille, S., Gagne, N., Belanger, L., Huot, J., Cimon, A., Dery, S., Jette, J.P., 2001. Effets de trois scénarios de régénération de la sapinière boréale sur les passereaux nicheurs, les petits mammifères et le lièvre d'Amérique. *Can. J. For. Res.* 31, 1312–1325.
- De Graaf, R.M., Hestbeck, J.B., Yamasaki, M., 1998. Associations between breeding bird abundance and stand structure in the White Mountains, New Hampshire and Maine. *For. Ecol. Manage.* 103, 217–233.
- DeMaynadier, P.G., Hunter, M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environ. Rev.* 3, 230–261.
- DeMaynadier, P.G., Hunter, M.L., 1997. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conserv. Biol.* 12, 340–352.
- DeMaynadier, P.G., Hunter, M.L., 2000. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. *J. Wildl. Manage.* 63, 441–450.
- Deuser, R.D., Shugart, H.H., 1978. Microhabitats in a forest-floor small mammal fauna. *Ecology* 59, 89–98.
- Dickson, J.G., Thompson, F.R., Conner, R.N., Franzreb, K.E., 1993. Effects of silviculture on neotropical migratory birds in central and southeastern oak pine forests. In: Finch, D.M., Stangel, P.W. (Eds.), *Status and Management of Neotropical Migratory Birds*. US Forest Service General Technical Report RM-229, pp. 374–385.
- Dobesberger, E.J., 1998. Stochastic simulation of growth loss in thinned balsam fir stands defoliated by the spruce budworm in Newfoundland. *Can. J. For. Res.* 28, 703–710.
- Drapeau, P., Leduc, A., Giroux, J.-F., Savard, J.-P., Bergeron, Y., Vickery, W.L., 2000. Landscape-scale disturbances and changes in bird communities of boreal mixedwood forests. *Ecol. Monogr.* 70, 423–444.
- Duvall, M.D., Grigal, D.F., 1999. Effects of timber harvesting on coarse woody debris in red pine forests across the Great Lakes States, USA. *Can. J. For. Res.* 29, 1916–1934.
- Edenius, L., Elmberg, J., 1996. Landscape level effects of modern forestry on bird communities in northern Swedish boreal forests. *Landsc. Ecol.* 11, 325–338.
- Eggstad, M., Enge, E., Hjeljord, O., Sahlgård, V., 1988. Glyphosate application in forest-ecological aspects. VIII. The effect on black grouse (*Tetrao tetrix*) summer habitat. *Scand. J. For. Res.* 3, 129–135.
- Ehnes, J.W., Shay, J.M., 1995. Natural recovery of burnt and logged plant communities in the Lake Winnipeg East Forest Section. Canada-Manitoba Partnerships Agreement No. 1992/93-5009, Canada Forest Service, Edmonton, Alta., p. 138.
- Elkie, P.C., Rempel, R.S., 2001. Detecting scales of pattern in boreal forest landscapes. *For. Ecol. Manage.* 147, 253–261.
- Enns, K.A., 1994. Effects of mechanical site preparation on wildlife in British Columbia. Forest Research and Development Agreement Report 218.
- Erskine, A.J., 1977. Birds of Boreal Canada. Canada Wildlife Service Report Series No. 41, Ottawa, Ont., Canada, 71 pp.
- Eschholz, W.E., Servello, F.A., Griffith, B., Raymond, K.S., Krohn, W.S., 1996. Winter use of glyphosate-treated clearcuts by moose in Maine. *J. Wildl. Manage.* 60, 764–769.
- Estades, C.F., Temple, S.A., 1999. Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantation. *Ecol. Appl.* 9, 573–585.
- Frelich, L.E., Lorimer, C.G., 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. *Biol. Conserv.* 34, 99–120.
- Gjerde, I., Saetersdal, M., 1997. Effects on avian diversity of introducing spruce plantations in the native pine forests of western Norway. *Biol. Conserv.* 79, 241–250.
- Gluck, M.J., Rempel, R.S., 1996. Structural characteristics of post-wildfire and clearcut landscapes. *Environ. Monit. Assess.* 39, 435–450.
- Haapenen, A., 1965. Bird fauna of the Finnish forests in relation to forest succession. *Anal. Zool. Fenn.* 2, 231–263.
- Hakkara, H., Korpimäki, E., Koivunen, V., Kurki, S., 1997. Boreal owl responses to forest management: a review. *J. Raptor Res.* 31, 125–128.
- Hansen, A.J., Spies, T.A., Swanson, F.J., Ohmann, J.L., 1991. Conserving biodiversity in managed forests. *Bioscience* 41, 382–392.
- Hansen, A.J., McComb, W.C., Vega, R., Raphael, M.G., Hunter, M., 1995. Bird habitat relationships in natural and managed forests in the West Cascades of Oregon. *Ecol. Appl.* 5, 555–569.
- Hanski, I., Moilanen, A., Gyllenberg, M., 1996. Minimum viable metapopulation size. *Am. Nat.* 147, 527–541.

- Hargis, C.D., McCullough, D.R., 1984. Winter diet and habitat selection of marten in Yosemite National Park. *J. Wildl. Manage.* 48, 140–146.
- Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. *For. Ecol. Manage.* 155, 81–95.
- Hayward, G.D., Hayward, P.H., Garton, E.O., 1993. Ecology of boreal owls in the northern Rocky Mountains. *Wildl. Monogr.* 124, 59.
- Hearnden, K.W., Millson, S.V., Wilson, W.C., 1992. A report on the status of forest regeneration: Ontario independent forest audit. Unpublished, available from: Ontario Ministry of Natural Resources, Sault Ste. Marie, Ont., Canada, 117 pp.
- Hector, A., Joshi, J., Lawlor, S.P., Spehn, E.M., Wilby, A., 2001. Conservation implications of the link between biodiversity and ecosystem functioning. *Oecologia* 129, 624–628.
- Henry, S.E., Ruggiero, L.F., 1993. Den use by and kit development of marten in Wyoming. In: Thompson, I.D. (Ed.), *Proceedings of the International Union Game Biology Conference*, vol. XXI, pp. 233–237.
- Hjeltjord, O., Sahlgard, V., Enge, E., Eggstad, M., Gronvold, S., 1988. Glyphosate application in forests—ecological aspects, VII. The effect on mountain hare use of a forest plantation. *Scand. J. For. Res.* 3, 123–127.
- Holling, C.S., 1992a. The role of insects in structuring the boreal landscape. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), *A Systems Analysis of the Global Boreal Forest*. Cambridge University Press, Cambridge, UK, pp. 170–191.
- Holling, C.S., 1992b. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.* 62, 447–502.
- Imbeau, L., Savard, J.-P., Gagnon, R., 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. *Can. J. Zool.* 77, 1850–1860.
- Innes, D.G.L., Bendell, J.F., Naylor, B.J., Smith, B.A., 1990. High densities of the masked shrew, *Sorex cinereus*, in jack pine plantations in northern Ontario. *Am. Midl. Nat.* 124, 330–341.
- Johnson, K.H., Vogt, K.A., Clark, H.J., Schmitz, O.J., Vogt, D.J., 1996. Biodiversity and the productivity and stability of ecosystems. *Trends Ecol. Evol.* 11, 372–377.
- Jung, T.S., Thompson, I.D., Titman, R.D., Applejohn, A.P., 1999. Habitat selection by forest bats in relation to mixedwood stand types and structure in central Ontario. *J. Wildl. Manage.* 63, 1306–1319.
- Kimball, A.J., Hunter, M.L., 1990. Intensive silviculture. In: Hunter, M.L. (Ed.), *Wildlife, Forests, and Forestry*. Prentice-Hall, Englewood Cliffs, NJ, pp. 200–234.
- Kirk, D.A., Hobson, K.A., 2001. Bird-habitat relationships in jack pine boreal forests. *For. Ecol. Manage.* 147, 217–243.
- Kirk, D.A., Naylor, B.J., 1996. Habitat requirements of the pileated woodpecker with special reference to Ontario. Ontario Ministry of Natural Resources, South Central Science and Technology Station, Technical Report No. 46, 49 pp.
- Lamothe, L., 1980. Birds of the Araucaria pine plantations and natural forests near Bulolo, New Guinea. *Corella* 4, 127–131.
- Land, D., Marion, W.R., O'Meara, T.E., 1989. Snag availability and cavity nesting birds in slash pine plantations. *J. Wildl. Manage.* 53, 1165–1171.
- Lautenschlager, R.A., 1993. Response of wildlife to forest herbicide application in northern coniferous ecosystems. *Can. J. For. Res.* 23, 2286–2299.
- Lavsund, S., 1981. Moose as a problem in Swedish forestry. *Alces* 17, 165–179.
- Lindenmayer, D.B., Cunningham, R.B., Pope, M.L., 1999. A large-scale experiment to examine the effects of landscape context and habitat fragmentation on mammals. *Biol. Conserv.* 88, 387–403.
- Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91, 3–17.
- Magura, T., Tothmeresz, B., Bordan, Z., 2000. Effects of nature management practice on carabid assemblages (Coleoptera: Carabidae) in a non-native plantation. *Biol. Conserv.* 93, 95–102.
- Martell, A.M., 1981. Food habits of southern red-backed voles (*Clethrionomys gapperi*) in northern Ontario. *Can. Field Nat.* 95, 325–328.
- Martell, A.M., 1983. Changes in small mammal communities after logging. *Can. J. Zool.* 61, 970–980.
- Martell, A.M., Radanyi, A., 1977. Changes in small mammal populations following clearcutting of northern Ontario black spruce. *Can. Field Nat.* 91, 41–46.
- MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. *Ecology* 42, 594–598.
- MacDonald, J.E., 1965. A bird census in red pine plantations and mixed stands in Kirkwood Township, Ontario. *Can. Field Nat.* 79, 21–25.
- McLaren, M.A., Thompson, I.D., Baker, J.A., 1998. Selection of vertebrate wildlife indicators for monitoring sustainable forest management in Ontario. *For. Chron.* 74, 241–248.
- Mikusinski, G., Angelstam, P., 1997. European woodpeckers and anthropogenic habitat change: a review. *Vogelwelt* 118, 277–283.
- Miller, G.R., Kinnaird, J.W., Cummins, R.P., 1982. Liability of saplings to browsing on a red deer range in the Scottish Highlands. *J. Appl. Ecol.* 19, 941–951.
- Monkkonen, M., Welsh, D.A., 1994. A biogeographical hypothesis on the effects of human-caused landscape changes in the forest bird communities of Europe and North America. *Anal. Zool. Fenn.* 31, 61–70.
- Moore, S.E., Allen, H.L., 1999. Plantation forestry. In: Hunter, M.L. (Ed.), *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press, Cambridge, UK, pp. 400–433.
- Morrison, M.L., 1992. Bird abundance in forests managed for timber and wildlife. *Biol. Conserv.* 60, 127–134.
- Moses, R.A., Boutin, S., 2001. The influence of clearcut logging and residual leave material on small mammal populations in aspen-dominated boreal mixedwoods. *Can. J. For. Res.* 31, 483–495.
- Moss, D., 1978. Song-bird populations in forestry plantations. *Quart. J. For.* 72, 5–13.
- Naylor, B.J., Bendell, J.F., 1983. Influence of habitat diversity on the abundance and diversity of small mammals in jack pine forests in Ontario. In: Wein, R.W., Riewe, R.R., Methven, I.R. (Eds.), *Resources and Dynamics of the Boreal Zone*. Assoc. Can. Univ. Northern Studies, Ottawa, Ont., Canada, pp. 295–307.
- Nilsson, S., 1979. Effect of forest management on the breeding bird community in southern Sweden. *Biol. Conserv.* 16, 135–143.

- Newton, M., Cole, E.C., Lautenschlager, R.A., White, D.E., McCormack, M.L., 1989. Browse availability after conifer release in Maine's spruce-fir forests. *J. Wildl. Manage.* 53, 643–649.
- Nordyke, K.A., Buskirk, S.W., 1991. Southern red-backed vole populations in relation to stand succession and old growth character in the central Rocky Mountains. *Can. Field Nat.* 105, 330–334.
- Norton, D.A., 1998. Indigenous biodiversity conservation and plantation forestry: options for the future. *New Zealand For.* 43, 34–39.
- Perera, A.H., Baldwin, D.J.B., 2000. Spatial patterns in the managed forest landscape of Ontario. In: Perera, A.H., Euler, D.L., Thompson, I.D. (Eds.), *Ecology of a Managed Terrestrial Landscape: Patterns and Processes of Forest Landscapes in Ontario*. UBC Press, Vancouver, BC, Canada, pp. 74–99.
- Peterken, G.F., Ausherman, D., Buchenau, M., Forman, R.T., 1992. Old growth conservation within British upland conifer plantations. *Forestry* 65, 125–144.
- Pimm, S.L., 1991. *The Balance of Nature?* University of Chicago Press, Chicago, IL.
- Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M., 1995. The future of biodiversity. *Science* 269, 347–350.
- Plosz, C., 1994. Bird species richness in managed coniferous woodlots in southern Ontario. M.Sc. Thesis, University of Guelph, Guelph, Ont., Canada.
- Potvin, F., Belanger, L., Lowell, K., 2000. Marten habitat selection in a clearcut boreal landscape. *Conserv. Biol.* 14, 844–857.
- Pough, F.H., Smith, E.M., Rhodes, D.H., Collazo, A., 1987. The abundance of salamanders in forest stands with different histories of disturbance. *For. Ecol. Manage.* 20, 1–9.
- Raymond, K.S., Servello, F.A., Griffith, B., Eschholz, W.E., 1996. Winter foraging ecology of moose on glyphosate-treated clearcuts in Maine. *J. Wildl. Manage.* 80, 753–763.
- Repenning, R.W., Labinsky, R.F., 1985. Effects of even-age timber management on bird communities of the longleaf pine forest in northern Florida. *J. Wildl. Manage.* 49, 1088–1098.
- Rempel, R.S., Elkie, P.C., Rodgers, A.R., Gluck, M.J., 1997. Timber-management and natural-disturbance effects on moose habitat: landscape evaluation. *J. Wildl. Manage.* 61, 517–524.
- Rochelle, J.A., Bunnell, F.L., 1979. Plantation management and vertebrate wildlife. In: Malcolm, D.C., Atterson, J. (Eds.), *The Ecology of Managed Forest Plantations*. Institute of Terrestrial Ecology, Edinburgh, UK, pp. 389–411.
- Rosenfield, R.N., Bielefeldt, J., Sonsthagen, S.A., Booms, T.L., 2000. Comparable reproductive success at conifer plantation and non-plantation nest sites for Cooper's hawks in Wisconsin. *Wils. Bull.* 112, 417–421.
- Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H., 1991. Wildlife and vegetation of unmanaged Douglas-fir forests. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-285, 533 pp.
- Russell, K.R., Van Lear, D.H., Guynn, D.C., 1999. Prescribed fire effects on herpetofauna: review and management implications. *Wildl. Soc. Bull.* 27, 374–384.
- Schaefer, J.A., Pruitt, W.O., 1991. Fire and woodland caribou in southeastern Manitoba. *Wildl. Monogr.* 116, 39.
- Settingington, M.A., Thompson, I.D., Montevercchi, W.A., 2000. Woodpecker abundance and habitat use in mature balsam fir forests in Newfoundland. *J. Wildl. Manage.* 64, 335–345.
- Siitonen, J., Martikainen, P., Puntilla, P., Rauh, J., 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *For. Ecol. Manage.* 128, 211–226.
- Simard, J.H., 2001. Habitat selection, ecological energetics, and the effects of changes in white pine forests on breeding red crossbills in Algonquin Provincial Park, Ontario. M.Sc. Thesis, McGill University, Montreal, Que., Canada, p. 130.
- Sippola, A.L., Siitonen, J., Kallio, R., 1998. Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. *Scand. J. For. Res.* 13, 204–214.
- Stelfox, J.G., Cormack, R.G.H., 1962. Effects of clearcut logging on wild ungulates in the central Albertan foothills. *For. Chron.* 38, 94–107.
- Stelfox, J.G., Lynch, G.M., McGillis, J.R., 1976. Effects of clearcut logging on wild ungulates in the central Albertan foothills. *For. Chron.* 52, 65–70.
- Su, Q., MacLean, D.A., Needham, T.D., 1996. The influence of hardwood content on balsam fir defoliation by spruce budworm. *Can. J. For. Res.* 26, 1620–1628.
- Sullivan, T.P., 1985. Effects of glyphosate on selected species of wildlife. In: Grossbard, E., Atkinson, D. (Eds.), *The Herbicide Glyphosate*. Butterworths, London, UK, pp. 186–199.
- Sullivan, T.P., Moses, R.A., 1986. Red squirrel populations in natural and managed stands of lodgepole pine. *J. Wildl. Manage.* 50, 595–601.
- Sullivan, T.P., Sullivan, D.S., 1982. Responses of small mammal populations to a forest herbicide application in a 20-year-old conifer plantation. *J. Appl. Ecol.* 19, 95–106.
- Sullivan, T.P., Sullivan, D.S., Lautenschlager, R.A., Wagner, R.G., 1997. Long-term influence of glyphosate herbicide on demography and diversity of small mammal communities in coastal coniferous forest. *Northwest Sci.* 71, 6–17.
- Sullivan, T.P., Lautenschlager, R.A., Wagner, R.G., 1999. Clearcutting and burning of northern spruce-fir forests: implications for small mammal communities. *J. Appl. Ecol.* 36, 327–344.
- Temple, S.A., Mossman, M.J., Ambuel, B., 1979. The ecology and management of avian communities in mixed hardwood-conifer forests. In: DeGraaf, R.M., Evans, K.E. (Eds.), *Management of Northcentral and Northeast Forests for Nongame*. United States Department of Agriculture, Forest Service, Northcentral Research Station, General Technical Report NC-51, pp. 132–151.
- Thomas, J.W., Anderson, R.G., Maser, C., Bull, E.L., 1979. Wildlife habitats in managed forests of the Blue Mountains of Oregon and Washington. United States Department of Agriculture, Forest Service, Agricultural Handbook, 553 pp.
- Thompson, I.D., 1988. Moose damage to pre-commercially thinned balsam fir stands in Newfoundland. *Ales* 24, 56–61.
- Thompson, I.D., 1994. Marten populations in uncut and logged boreal forests in Ontario. *J. Wildl. Manage.* 58, 272–280.

- Thompson, I.D., 2000. Forest vegetation of Ontario: factors influencing landscape change. In: Perera, A.H., Euler, D.L., Thompson, I.D. (Eds.), *Ecology of a Managed Terrestrial Landscape: Patterns and Processes of Forest Landscapes in Ontario*. UBC Press, Vancouver, BC, Canada, pp. 30–53.
- Thompson, I.D., Colgan, P.W., 1991. Prey choice by marten during a decline in prey abundance. *Oecologia* 83, 443–451.
- Thompson, I.D., Curran, W.J., 1993. A reexamination of moose damage to balsam fir—white birch forests in central Newfoundland: 27 years later. *Can. J. For. Res.* 23, 1388–1395.
- Thompson, I.D., Curran, W.J., 1995. Habitat suitability for marten of second-growth balsam fir stands in Newfoundland. *Can. J. Zool.* 73, 2059–2064.
- Thompson, I.D., Hogan, H.A., Montevecchi, W.A., 1999. Avian communities of mature balsam fir forests in Newfoundland: age-dependence and implications for timber harvesting. *Condor* 101, 311–323.
- Ure, D.C., Maser, C., 1982. Mycophagy of red-backed voles in Oregon and Washington. *Can. J. Zool.* 60, 3307–3313.
- Virkkala, R., 1991. Population trends of forest birds in a Finnish Lapland landscape of large habitat blocks: consequences of stochastic environmental variation or regional habitat alteration? *Biol. Conserv.* 56, 223–240.
- Voigt, D.R., Baker, J.A., Rempel, R.S., Thompson, I.D., 2000. Forest vertebrate response to landscape-level changes in Ontario. In: Perera, A.H., Euler, D.L., Thompson, I.D. (Eds.), *Ecology of a Managed Terrestrial Landscape: Patterns and Processes of Forest Landscapes in Ontario*. UBC Press, Vancouver, BC, Canada, pp. 198–234.
- Wedeles, C.H.R., Van Damme, L., 1995. Effects of clearcutting and alternative silvicultural systems on wildlife in Ontario's boreal mixedwoods. NODA/NFP Technical Report TR-19, Canada Forest Service, Sault Ste. Marie, Ont., Canada, p. 56.
- Welsh, H.H., Droege, S., 2001. A case for using Plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. *Conserv. Biol.* 15, 558–569.
- Welsh, C.J.E., Healy, W.M., 1993. Effect of even-aged timber management on bird species diversity and composition in northern hardwoods of New Hampshire. *Wildl. Soc. Bull.* 21, 143–154.
- Welsh, D.A., Lougheed, S.C., 1996. Relationship of bird community structure and species distributions to two environmental gradients in the northern boreal forest. *Ecography* 19, 194–208.
- Wigley, T.B., Baughman, W.M., Dorcas, M.E., Gerwin, J.A., Gibbons, J.W., Guynn, D.C., Lancia, R.A., Leiden, Y.A., Mitchell, M.S., Russell, K.R., 2000. Contributions of intensively managed forests to the sustainability of wildlife communities in the south. In: *Sustaining southern forests: the science of forest assessment*. USDA Forest Service, Southern Forest Research Assessment. Available on line at: <http://www.srs.fs.fed.us/sustain/conf/>.
- Wilkins, R.N., Peterson, N.P., 2000. Factors related to amphibian occurrence and abundance in headwater streams draining second-growth Douglas-fir forests in southwestern Washington. *For. Ecol. Manage.* 139, 79–91.
- Willson, M.F., Comet, T.A., 1996. Bird communities of northern forests: ecological correlates of diversity and abundance in the understory. *Condor* 98, 350–362.
- Yamamura, Y., 2002. Biodiversity and stability of herbivore populations: the influence of the spatial sparseness of food plants. *Popul. Ecol.* 44, 33–40.

